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Executive summary

The Study Group on Multispecies Assessment in the North Sea (SGMSNS) has held two meetings, the last of which was held in April 2005. SGMSNS was mainly tasked with producing an updated keyrun of the North Sea MSVPA and attempting to identify the future direction of multispecies assessment and advice in ICES.

The MSVPA keyrun suffers from the same problems of inaccurate catch data (cod) and methodology (whiting) the same as with the single species assessment. Data requested from the ICES Working Group on Seabird Ecology (WGSE) and the Working Group on Marine Mammal Ecology (WGMME), on sea birds and marine mammals population numbers, diet and consumption rations were not available yet and therefore could not be included in the new keyrun. New estimates of consumption rates for the main predator fish species were presented and used in the keyrun. Compared to the previous used values the rations have increased for cod and mackerel and decreased for saithe and especially whiting.

The main difference between the 2003 and 2005 keyrun results is due to the re-introduction of grey gurnard and changes in predator rations. Gurnard mainly affects the predation mortalities of 0-group cod and whiting, which are two-three fold higher in this year's keyrun. The predation mortality on the prey species sandeel, herring, sprat and Norway pout have increased in this year's keyrun, mainly due to the increase in mackerel and cod rations.

The keyrun results are considered more uncertain in the most recent years for various reasons. There has been a shift of dominance between the "traditional" MSVPA predators (cod, whiting, saithe and haddock) towards "other predators" (mainly mackerel, horse mackerel and grey gurnards), for which rather uncertain stock abundances exists. Stomach sampling has historically been focused on the "traditional" MSVPA predators and for some "other predators" the number of stomach samples is quite low. The predation mortality for the whole assessment period 1963–2003 is based on stomachs sampled for the years 1981–1991. This dataset might not reflect the diet and stock distributions today, and this could bias the estimation of predation mortality.

It was concluded that there is still a long way to go until 0-group fish dynamics can be reliably modelled in multispecies models.

Some progress in Ecopath with Ecosim modelling of the North Sea ecosystem using in- and output from the keyrun has been made since the last Study Group meeting.

The future of Multispecies modelling in ICES was discussed. It is clear that ICES cannot neglect multispecies interactions in its future work where the ecosystem approach to management, stock recovery and definition of long-term goals and management will be in focus. In addition, most of the scientific work on multispecies interactions takes place in projects outside ICES and therefore ICES needs a forum for the integration of this external research into its advisory procedures.

The SGMSNS proposes that a new Working Group on Multispecies Assessment should be established. The research in the WG should not be confined to a single modelling approach but should cover alternative models of multispecies interactions and in a wider geographical area. The new WG should meet annually. Every third meeting should be dedicated to constructing an updated key run with new catch data. The intervening years should be used to work on specific themes, drawing in expertise from other scientific disciplines and from outside the ICES community. Alternatively, the WG could meet annually for keyrun updates in conjunction with a series of themed workshops.

1 Introduction

1.1 Terms of Reference

The **Study Group on Multispecies Assessment in the North Sea** [SGMSNS] (Co-Chairs: M. Vinther, Denmark, and E.D. Bell, UK) will meet at ICES Headquarters from 5–8 April 2005 to:

- a) prepare a 'definitive' and fully revised 4M model key-run, incorporating any revisions in consumption rates or other available data;
- b) re-evaluate the importance of mackerel as an MSVPA predator in the North Sea;
- c) incorporate the biomass data, consumption rates and diet compositions provided by the Working Group on Seabird Ecology (WGSE), and the Working Group on Marine Mammal Ecology (WGMME) for marine mammals and seabirds. Evaluate the importance of newly introduced predators (e.g., harbour seals), and whether these affect 4M outputs;
- d) re-examine the issue of whether 0-group fish can adequately be modelled using the 4M or other multispecies modelling approaches;
- e) address 'applied' and specific questions posed intersessionally by ACFM;
- f) perform a data fitting exercise using the North Sea 1991 EwE model. The fitting exercise will require input (survey CPUE) and output data (MSVPA estimated biomasses) from the updated 4M key-run (Term of Reference a);
- g) examine the need within ICES and develop a strategy for multispecies stock assessment and subsequent multispecies advice on management issues;
- h) prepare a draft resolution for a new expert group, should the outcome of g) identify the need for this.

SGMSNS will report by 18 April 2005 for the attention of the Resource Management and Living Resources Committees, ACFM, and ACE.

1.2 Scientific justification for the Study Group

The ICES Multispecies Assessment Working Group (MAWG) was disbanded in 1997, because it was thought that there was no need for routine multispecies stock assessment and advice on fisheries management issues. Nevertheless, it was since been widely recognised that the development of viable long-term management strategies depends on a good understanding of species and fleet interactions, and recent ongoing requests for advice reflects the continuing interest in this field.

The Study Group on Multi-Species Assessment in the North Sea (SGMSNS) is tasked with producing an updated key-run of the North Sea MSVPA and attempting to identify the future direction of multispecies work in the context of the North Sea. SGMSNS had its first of two proposed meetings in August 2003 and this second meeting in April 2005.

1.3 Working papers and background documents

Three working papers were presented to the group and are given in full in the annexes as follows.

- Annex 3: The Feasibility of including harbour porpoise *Phocoena phocoena* as a predator in MSVPA
- Annex 4: An analysis of the grey gurnard implementation in the North Sea MSVPA
- Annex 5: Are we able to model 0-group fish?

2 Update and revision of 4M program and input data

2.1 The 4M-package

The 4M package (Multispecies, Multi-fleet, Multi-area Model-package) (Vinther *et al.* 2002) was used to run MSVPA and MSFOR at this study group. The aim of 4M has been to create an integrated-software-system handling model input, the models, and analysis and presentation of output. Basically 4M combines the modules MSVPA and MS-FORECAST written in ANSI C with a SAS environment for data management, analysis and presentation.

2.2 VPA related input data

The compilation of catch numbers and mean weight at age by quarter for use in North Sea Multi Species SG is part of the ToR for the WGNSSK and HAWG. Consequently, data should have been available in the WG reports.

2.2.1 Catch data

For the species sole, plaice, Norway pout, sandeel, herring and sprat, catch data were copied from the relevant ICES WG or made available from the single-species stock coordinators. The ICES assessment for plaice now includes an estimate of discards for the whole assessment period. It was not possible to obtain updated quarterly catch data for this species, however it would have made very little difference to the outputs of MSVPA, as this species is not a predator within MSVPA and it is hardly eaten.

The Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK) had not compiled quarterly catch data for cod, haddock, saithe and whiting for 2002 and 2003 as specified in the ToR for WGNSSK. Hence it was not possible to obtain data from the stock coordinator for these species. As an alternative, the annual catches were used and it was assumed the seasonal distribution of catches in 2002-and 2003 was equal to the average quarterly catch distribution for 1997–2001. For stocks with a wider spatial coverage than the North Sea (e.g., cod in area IV, IIIa and VIId) the catch numbers were downscaled by the proportion of the total stock catch weight historically taken in the North Sea. Average quarterly mean weights from 1997–2001 were used as mean weights for 2002–2003.

The WGNSSK (in 2004) estimated "missing caches" of cod for the last 10 years. Data were not available by quarter, therefore new catch numbers from the WG were apportioned in accordance with the relative quarterly distribution of catches assumed in earlier runs of MSVPA.

2.2.2 Terminal fishing mortality

Estimation of terminal fishing mortalities for use in MSVPA was carried out using multispecies tuning (Vinther, 2001). This procedure involves the iterative exchange of natural mortalities from the MSVPA and terminal F from ICES tuning packages (XSA, ICA and SXSA) until convergence. The tuning exercise utilised the same CPUE time-series and options as used by the single-species assessment WGs. However the modified ADAPT assessment used for the cod assessment in 2004, was not implemented in the 4M-tuning, and XSA was used instead. No whiting assessment was provided by WGNSSK for 2004, however XSA was used in the 4M model.

Where the single-species assessment did not include the 0-group (e.g., cod), a dummy catch number and a terminal F were required for the terminal year. These were created from results such that the estimated 0-group numbers followed the same trend as that suggested by the single species working group.

2.3 Biomass of "Other predator"

2.3.1 Mackerel

There are two components to the mackerel stock in the North Sea, a resident population and a migratory population. Historically the resident population was very large (ca. 2.5 million tonnes, Hamre (1978)), but since the 1970s, it has been greatly reduced (36–110 thousand tonnes SSB, ICES (2002a)). The last North Sea egg survey was carried out in 2002. Based on this survey the SSB was estimated at 210,000 tons, which is considered uncertain due to restricted survey time and the application of a standardised fecundity estimate (ICES CM 2005/ACFM:08). The severe decline in the resident North Sea component of the mackerel stock has been partially compensated for by influxes of the "Western Mackerel" component into the northern North Sea during the second half of the year since the 1970s. It is not possible to distinguish between the two stock components in the catches. However, due to the differing time scales of residency, different spatial distribution and diet, MSVPA treats the two stocks components differently.

Revised stock size estimates were obtained come from the Mackerel, Horse Mackerel, Sardine and Anchovy Working Group [WGMHSA]. Previously, assessment was carried out by the WG for the "Western Mackerel" separately. The estimated stock numbers in combination with an assumed known stock proportion within the North Sea were then used as input for MSVPA. At the 2004 WGMHSA meeting (ICES CM 2005/ACFM:08), the only assessment presented was for the combined North East Atlantic (NEA) mackerel stock (including North Sea, Western and Southern components). WGMHSA calculated the historic stock mean weight from the observed mean weight by stock component and a weighting factor for each component. These weighting factors (Table 2.1) were used to calculate the "MSVPA" stock numbers by component.

The MSVPA North Sea component is calculated as total NEA mackerel numbers times the North Sea proportion times the proportion of North Sea mackerel resident in the North Sea (Table 2.1). The last set of numbers has previously been given by WGMHSA, but has not been updated since 1987. A similar calculation is done for the Western component, again with the latest update of the proportion within the North Sea from 1987. This approach was used in previous MSVPA assessments, and is used again now. However, independent stock surveys in the North Sea (IBTS and EGFS) indicate a higher current abundance of mackerel in the 1st and 3rd quarters since 1992, specifically in the third quarter in the southern North Sea (Figures 2.1 and 2.2). Since this increase is not reflected in the trend in the total NEA mackerel stock, it was assumed that a higher fraction of the total stock was residing in the third quarter in the North Sea since 1992. First quarter fractions were not increased since the mackerel occur mainly in the northern North Sea at that time and the northern North Sea survey index of mackerel was regarded as much more unreliable than the southern North Sea indices. The reasoning was that mackerel catchability with the GOV trawl in the IBTS was assumed to be much lower in the northern areas than in the shallower southern North Sea For in increase in abundance of mackerel in the southern North Sea in the 1990s see also (Beare et al. 2004).

The fractions of Western Mackerel present in the North Sea in the 3rd quarter were increased for the age 1 from 30% to 50, and for ages 2 and 3+ from 50% to 75%. To coarsely track the survey time series, in the following years the fractions were decreased in 2% steps until they ended at 35% and 55%, 55% in 2002, and 2003. However, even assuming that the whole stock resided in the North Sea in the late 1990s would not bring the calculated abundance in agreement with the survey data, making the applied correction rather arbitrary.

The NEA mackerel assessment gives a full stock number matrix from 1980 and onwards. MSVPA stock numbers of North Sea and Western mackerel were updated for the same period.

Table 2.1: Proportion of the North East Atlantic mackerel by components. (Data from Table 2.4.4.2 in ICES CM 2005/ACFM:08)

İ	North Sea	Western	Southern
 Year	-+ 		+
1972	0.254	0.618	0.128
1973	0.249	0.624	: :
1974	0.221	0.651	
1975	0.205	0.668	!
1976	0.201	0.671	
1977	0.177	0.695	
1978	0.136	0.736	0.128
1979	0.125	0.747	0.128
1980	0.116	0.756	0.128
1981	0.081	0.786	0.133
1982	0.080	0.792	0.128
1983	0.074	0.798	0.128
1984	0.037	0.835	0.128
1985	0.037	0.835	0.128
1986	0.037	0.835	0.128
1987	0.037	0.835	0.128
1988	0.037	0.835	0.128
1989	0.037	0.835	0.128
1990	0.037	0.835	0.128
1991	0.037	0.835	0.128
1992	0.037	0.835	0.128
1993	0.037	0.835	0.128
1994	0.037	0.835	0.128
1995	0.037	0.835	0.128
1996	0.037	0.835	0.128
1997	0.037	0.835	0.128
1998	0.018	0.773	0.209
1999	0.018	0.773	
2000	0.018	0.773	0.209
2001	0.028	0.848	
2002	0.028	0.848	
2003	0.028	0.848	0.124

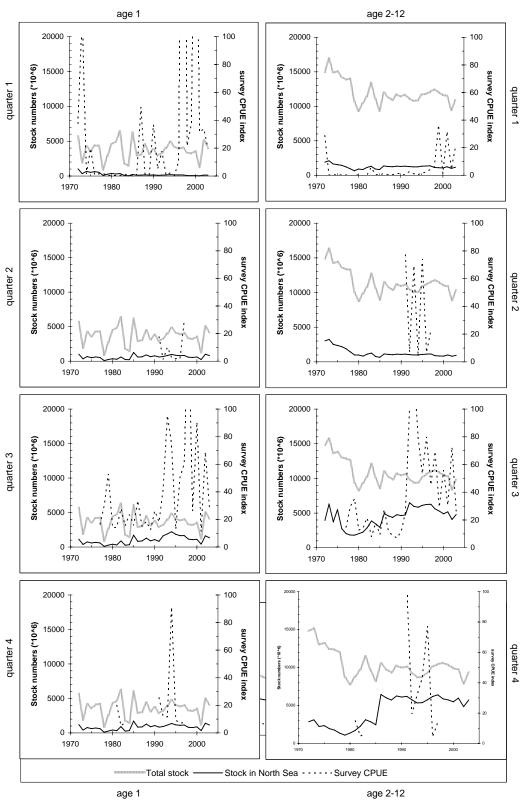


Figure 2.1 Time trends in the NEA Mackerel stock (WGMHSA), the part of the stock residing in the North Sea (calculation based on table 2.3.1), and survey indices of mackerel abundance in the North Sea.

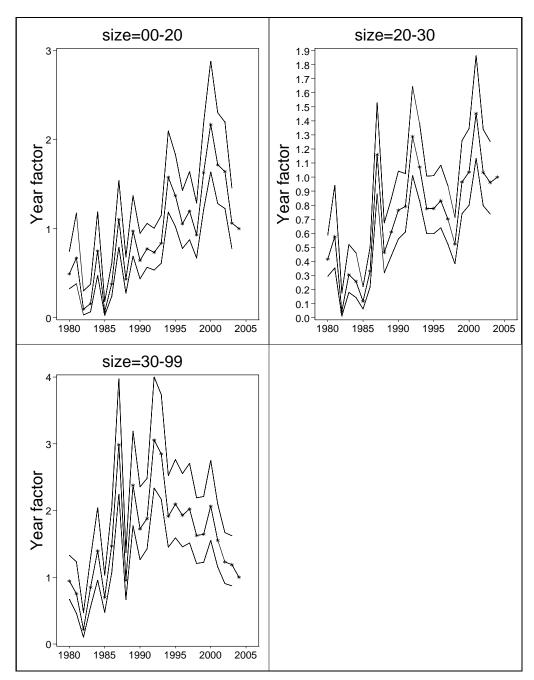


Figure 2.2: Estimate of year effect (overall year abundance index, log values) of *Raja radiata* by size class (cm). The graphs show estimated value and 95% confidence limits.

2.3.2 Horse mackerel

For many years the WGMHSA considered the horse mackerel in the north east Atlantic as separated into three stocks: the North Sea, the Southern and the Western stocks. The Horse mackerel included in the 2003 MS key-run included the resident North Sea stocks and a time variable proportion of the Western Stock.

A study of stock structure of horse mackerel from an holistic point of view within the western, the southern, the North Sea and the Mediterranean areas recently been carried out as part of an EU funded project (HOMSIR, QLK5-Ct1999–01438). The project concluded that the former stock definition previously used needs revision. However, based on spatial and temporal distribution of the horse mackerel fishery WGHMSA continued in 2005 to allocate catches to the three stock components. WGHMSA considered that the assessments made on stocks as ex-

ploratory and no tables with e.g., estimated stock number were available to be used in the keyrun. Consequently the value estimated for 2001 in the SGMSNS 2003 keyrun, was rolled-over and used in both 2002 and 2003. Horse mackerel could not be excluded completely from the new key run because they have been shown to consume substantial quantities of 0-group whiting.

2.3.3 Seabirds

Seabird numbers were provided by WGSE (ICES, 2005). Numbers of birds at sea were calculated from the European Seabirds at Sea Database (ESAS) version 4.1 and from published accounts on breeding population sizes along the North Sea coasts. The ESAS database 4.1 contains data from seabirds at sea counts over the period 1979 to 2004. Due to unequal coverage over years and seasons, it was only considered possible to estimate numbers for each quarter for two periods, 1979–1991 and 1992–2004. Data were calculated separately for six subregions following Tasker and Furness (1996), reduced slightly to match the overall area defined for the MSVPA, and were then summed. As seabirds are partly on land while breeding and also at other times of the year, numbers were corrected following largely the procedure by Tasker and Furness (1996). Energy requirements for chicks were also estimated and expressed as numbers of adults as these are not covered by the energy budgets for adults. All these numbers derived from land/colonies were then added to the numbers calculated for the sea areas from the ESAS database. Data for the years before 1979 were taken from the period 1979–1991.

Previous population numbers used by the North Sea MSVPA were derived solely from counts of breeding pairs at colonies. The new methodology described above has resulted in a significant increase in the estimate of feeding seabirds in the North Sea by up to a factor of five. The sudden switch in quarterly distribution between the two sections of the time series was considered by SGMSNS to be ecologically unrealistic. It was therefore decided to use a smoothing function to cover the transition period and 5 year moving window average was applied.

These new stock numbers were used in an exploratory run but are not included in the key run.

2.3.4 Marine mammals

There is currently a great deal of uncertainty as to total grey-seal population numbers in the North Sea, however SGMSNS decided that it should no longer assume a 6% per year increase in grey-seal numbers, as there are some indications that population growth may now be levelling off. New population estimates were introduced for the years 2001, 2002, 2003 and these were obtained from WGMME (2005) and the annual reports of the UK Special Committee on seals (SCOS - smub.st-and.ac.uk/CurrentResearch.htm/scos.htm).

New population numbers for harbour seals were not available from WGMME, despite being included among the group's ToRs for 2004. Consequently, harbour seals could not be included in the 2005 MSVPA key-run (although specified as a ToR for SGMSNS in 2005).

A working paper was presented (Pinnegar *et al.*, 2005) focussing on the feasibility of including harbour porpoise (*Phocoena phocoena*) within the MSVPA key run. Porpoise are the most common species of cetacean in the North Sea and their population numbers may exceed 200,000 animals, or 9500 tones. Assuming an average consumption rate of around 3.5 kg per day, then porpoises may remove in excess of 290 000 tones of fish every year (mostly whiting and sandeel), substantially more than is removed by seals. It was concluded that important advances have been made since the 2003 SGMSNS meeting and it would now almost certainly possible to provide sufficient input data to add harbour porpoises to the North Sea MSVPA model. In 2005 a second SCANS survey will be conducted and hence revised abun-

dance estimates will come available, in addition size-disaggregated stomach-contents data are now available by quarter (season) and geographic area (Santos *et al.*, 2004).

2.3.5 Gurnards and R. radiata

The methodology developed at the 2002 meeting (ICES, 2002) to estimate the population abundance was also applied this year. The method is based on GLM (assuming a Poisson distribution and a log-link function) analysis of IBTS CPUE by size class with year, quarter, gear and roundfish area as explanatory variables. The estimated year and quarter effects are then used to estimate of the annual and quarterly abundance given an assumed mean biomass for the whole period.

ICES has reorganised and quality checked IBTS data for the period since 1983. This updated dataset was used as basis for the estimation of Gurnard and *Raja radiata* population numbers for the period since 1983. To exclude hauls where gurnards or *R. radiata* were not recorded only haul records with the bycatch species record code equal to '1' and '2' (all bycatch species recorded) were included. For some vessels, an extra filtering of data was necessary even though the bycatch code indicated that all species were recoded.

Gurnards

The vessel Isis (ISI) had no catch of grey gurnards recorded for 1983–87, a bycatch code that showed that not all species were recorded in 1988, and very limited catch for 1989. From 1991 and onwards grey gurnards were recorded on every trip. Consequently "Isis" data from before 1991 were deleted.

The gear "HOB" was utilised by one vessel in one year with very low catch rate of gurnards. All records with gear "HOB" were deleted.

A preliminary GLM run showed that the year effect estimate before 1970 had high variance, mainly because of few hauls with a poor spatial coverage for the individual years. Therefore, the years before 1970 were aggregated into one pool and the year effect for 1963–1970 was assumed constant over the period and estimated from that pool of data.

Grey gurnard was excluded completely from the 2003 MSVPA key run (ICES, 2003) but has been reintroduced in the 2005 key-run.

R. radiata

No catch of *R. radiata* was taken in the few IBTS hauls using the gears "INT" and "GRT" and consequently these hauls were deleted.

A preliminary GLM run showed that the year effect estimate for years before 1980 had an extremely high variance, mainly because of few hauls with a poor spatial coverage for the individual years. The years before 1980 were lumped into one pool and the year effect for 1963–1980 was estimated from that pool of data combined.

2.4 Stomach content data

The 1997 report of MAWG (ICES, 1997a) provides an extensive overview of historic uses of different sets of stomach content data at different occasions and of various major revisions over time.

2.4.1 Mackerel data, 1981

At the Multispecies Assessment Working Group – MAWG in 1997 (ICES, 1997a) it was decided to exclude mackerel data sampled in 1980–1983 from the key-run as the standard program, ISR, for compilation of stomach contents data had not been used. Before the 2005 meeting an attempt was made to compile the 1981 mackerel data using "ISRapproach" as had been used to compile the 1991 data. However, due to missing stock distribution data on the North Sea and the Western mackerel components this proved not to be possible. Consequently, the 1981 data was included in the 2005 key-run in it's un-standardised form, but some exploratory analyses were carried out to assess the implications.

2.4.2 Seabirds

The North Sea is utilised as a feeding ground by 38 species of seabird for at least part of the year. 22 of these species are breed around the margins of the North Sea. However, 94% of the energy usage by seabirds in the North Sea is taken by just eight species (and no other species takes more than 2% of the consumption). Following Tasker and Furness (1996) WGSE based the food consumption estimates on these top eight species. These eight species are:

1. Fulmar, 2. Guillemot, 3. Herring Gull, 4. Kittiwake, 5. Great black-backed gull, 6. Gannet, 7. Puffin, 8. Razorbill and are the same as used in previous runs of MSVPA.

Dominant seabirds in the North Sea, ordered by percentage of total seabird consumption (Tasker and Furness 1996):

SPECIES	PERCENTAGE CONSUMPTION
1. Fulmar	28.1
2. Guillemot	26.3
3. Herring Gull	11.6
4. Kittiwake	7.9
5. Great black-backed gull	7.7
6. Gannet	7.0
7. Puffin	2.8
8. Razorbill	2.6

Quarterly dietary data were provided by WGSE for each of these species in terms of percentage of diet for the following food types. Sandeel, Herring, Cod, Haddock, Whiting, Plaice, Saithe, Mackerel, Sole, Sprat, Norway Pout, Discards and Other.

WGSE also provided the quarterly consumption (in weight) of each bird species for Sandeel, Herring, Haddock, Whiting, Plaice, Saithe, Mackerel, Sprat, Norway Pout, Sole and Cod. These data did not, however, include the discard component and it is unclear if the rations include a discard component.

Data on the size distribution of prey was available for Guillemots, but this only went as far as minimum, mean and maximum lengths by prey type. There was not enough information in these values to construct prey numbers at length and hence prey numbers at age as required by MSVPA.

These data on seabird diet arrived from WGSE whilst the SG was in progress, hence there was not time to clarify several issues in order to properly utilise the new data. Clearly there will need to be several iterations of information exchange with WGSE before we can arrive at new consumption/ration estimates of seabirds for use within MSVPA. The EU funded project BE-CAUSE includes the construction of new bird diet data.

2.4.3 Marine mammals

Revised stomach content data for grey seals and new diet composition estimates for harbour seals were not available from WGMME in 2004/5. However, in order to address the data request from SGMSNS, WGMME has now committed itself to contacting North Sea marine mammal research organizations to ascertain the type of diet data available for the most recent five-year period (1999–2003), and data likely to become available during the current year. In the meantime, SGMSNS continued to use the grey seal consumption estimates provided by Hammond *et al.* (1997) for the 2005 key-run. Extensive diet sampling programmes for both grey seals and harbour seals are currently being conducted and these data should come available in 2005–2006.

A working paper was presented (Pinnegar *et al.* 2005) focusing on the feasibility of including harbour porpoise (*Phocoena phocoena*) within the MSVPA (based on that provided by Hammond *et al.* in 1997 for grey seals). Size-disaggregated stomach-contents data are now available by quarter (season) and geographic area (Santos *et al.* 2004; Benke *et al.* 1998; Martin 1996). This weight or length-stratified data could be readily used to produce age-stratified input data intersessionally for MSVPA in 2006.

2.5 Consumption Rates

2.5.1 Gadoids

2.5.1.1 Introduction

The mean food consumption rate \hat{C} over time and predator population can be described by the mean evacuation rate of the stomach contents of a representative section of the predator population (Pennington, 1995). Recent research has shown that, basically, instantaneous evacuation rate dS_t/dt in predatory gadoids relates to the square root of current stomach content mass. Then,

$$\hat{C} = \overline{\rho S^{\frac{1}{2}}}$$

where S and ρ are total mass and evacuation rate constant, respectively, of the stomach content of each individual sampled in the field (Andersen, 2001).

A simple, mechanistic gastric evacuation model has been established following a geometric interpretation of the square root relationship (Andersen and Beyer, *in press*) where digestion is described as a surface-dependent process. Primary and interactive effects of size, energy density and resistance to digestion of individual prey in a stomach were described by the model. Model predictions of the results from experiments on gastric evacuation of meals composed of different prey types demonstrated the capability of this model, unlike previously applied model principles, to predict evacuation of mixed meals involving the three above-mentioned prey characteristics. The study furthermore illustrated that estimates of food ration might be severely biased by using improperly formulated effects of prey characteristics on gastric evacuation, and demonstrated that the new model holds the potential to predict food rations and diet composition for wild populations of predatory gadoids.

Because of the interactive effects of the different prey characteristics it is recommended to use the evacuation model to data on the content of each individual stomach estimating food rations in order to avoid the possibility of introducing excessive bias. This was not possible to do here because the stomachs sampled by ICES generally were pooled into predator length groups from each haul. Data on mean stomach content from each individual haul probably give a more realistic picture of prey composition of individual stomachs than do those obtained from

averaging over larger geographical areas (ICES squares, round fish areas, and total North Sea).

In an initial exercise, food rations were estimated by application of the new evacuation model to information about stomach contents at all levels of averaging using stomach data from 1991 to evaluate the effects of data aggregation level. This included estimates of individual prey species/groups as well as total rations. Further, the new estimates of total ration obtained from the 1991 stomach data (application of the new evacuation model to average data at the level of round fish area) were compared with the estimates previously used by ICES. Finally, smoothed values of total quarterly food rations were provided for all four gadoids by application of GLM-model to estimates obtained from stomach data for all stomach sampling years.

2.5.1.2 Estimation of food rations

According to the new evacuation model, the contribution of a stomach to the consumption rate $(g \cdot h^{-1})$ of each prey item *i* can be described by:

$$\hat{C}_{i} = \rho_{i,E} E^{-0.86} b_{i} S^{1/2} = \rho_{i,E} \left(\frac{\sum \rho_{i,E} b_{i} E_{i}}{\sum \rho_{i,E} b_{i}} \right)^{-0.86} b_{i} S^{1/2}$$

and the contribution of the stomach to the estimate of total food consumption rate becomes

$$\hat{C} = \sum C_i$$

where $\rho_{i,E}$ is the basic evacuation rate of prey i, which reflects the resistance to digestion of the prey. Through feed back mechanisms from the proximal intestine, this rate is modulated by the energy density E (kJ·g⁻¹) of the evacuated chyme at the time of sampling. E_i is the mean energy density of prey i, and the composition of the chyme is determined by the individual values of $\rho_{i,E}b_i$, where b_i is the contribution of each prey to the surface of total stomach content exposed to digestion as determined from the cylinder abstraction of the square root relationship by Andersen and Beyer ($in\ press$). The value of the basic evacuation rate $\rho_{i,E}$ is similar for all fish prey (Andersen, 2001).

Here, food rations were estimated by use of information from the international sampling surveys undertaken by ICES and contained in the North Sea stomach data base. The stomach contents data were generally pooled by predator size. Therefore, only mean values \overline{S} of stomach contents were available, and size measures of individual prey items in the stomachs were not generally included in the data base. Thus, the effects of prey size could not be taken into consideration, and the concept of surface contributions b_i of individual prey items by Andersen and Beyer (*in press*) had to be abandoned - and replaced by the mean mass contributions \overline{a}_i of individual prey types. The above expression for food consumption rate of prey type i was therefore replaced by

$$\hat{C}_{i} = \overline{\rho}_{i,E} \left(\frac{\sum \overline{\rho}_{i,E} \overline{a}_{i} \overline{E}_{i}}{\sum \overline{\rho}_{i,E} \overline{a}_{i}} \right)^{-0.86} \overline{a}_{i} k \overline{S}^{\vee_{2}}$$

The k factor was introduced to correct for $\overline{S}^{\frac{1}{2}}$ being different from $\overline{S}^{\frac{1}{2}}$ unless all values of S are equal. k was refined splitting the influence of the S variation into the frequency of empty stomachs (S=0) and the frequency distribution of S from stomachs with food. This way, the information about the frequency of empty stomachs in the pooled ICES data was used to modulate the value of k by $k=k_Fp_F^{\frac{1}{2}}$ where k_F was calculated from S values of the non-empty stomachs of representative sets of individual stomachs obtained from other sources, and p_F is the proportion of non-empty stomachs within the relevant pooled set of ICES stomach

data (anon., 2003). The Calculations from data on various predatory gadoids gave relatively similar values of k_F (anon., 2003) and a general value of 0.85 is applied here.

The mean basic evacuation rate constant $\overline{\rho}_{i,E}$ for prey type i was expanded by $\overline{\rho}_{i,E} = \rho_{i,LTE} \overline{L}^{1.4} e^{0.08\overline{T}}$ as a function of mean predator length \overline{L} (cm) and temperature \overline{T} (°C). Estimates of $\rho_{i,LTE}$ of fish prey in stomachs of the gadoids whiting, saithe and cod were obtained by Andersen (2001) and for evacuation in haddock by A. P. Robb (Marine Laboratory, Aberdeen, unpublished results). Robust exoskeletons of a variety of different invertebrates are known to increase the resistance to digestion compared to fish prey whereas soft-bodied invertebrates like annelids are of lesser resistance (Bromley, 1994). Values of evacuation rate for relevant groups of these types of prey were obtained from different published as well as unpublished sources. Data on the geographical distribution of quarterly mean bottom temperature [estimated by J. –P. Herrmann, Hamburg University, from a 3-D circulation model of the North Sea (Pohlmann 1996)] and abundance of the gadoid predator by age in 1991 [from ICES International Bottom Trawl Survey (IBTS) database, Copenhagen] were combined to estimate mean temperatures \overline{T} at the aggregation level of stomach data to which the evacuation model was applied.

The quarterly mean energy density \overline{E}_i of prey type i was estimated from its size class distribution in the stomachs combined with the energy density by prey size class (Pedersen and Hislop, 2001, and unpublished data).

Quarterly prey type specific and total food rations (g) were estimated as 2190 h \times \hat{C}_i g·h⁻¹ and 2190 h \times Σ \hat{C}_i g·h⁻¹, respectively.

The coefficient of variation (CV) for each estimate of total food ration was obtained by bootstrapping.

2.5.1.3 The new food ration estimates

In general, the new estimates of total quarterly food ration in 1991 obtained for the four gadoid predators were not influenced substantially by the level of data aggregation at which the gastric evacuation model was applied (Table 2.2). This is in accordance with the results of Andersen and Beyer (in prep), who found that different ways of modelling the effects of prey characteristics on gastric evacuation did only to a limited extent influence the estimate of total food rations. The estimates of consumption of individual prey groups/species by the gadoid predators were, however, affected by the applied level of data aggregation. Substantial differences were found in cases where the prey differed significantly by their energy densities. For example, the proportions of fat herring consumed by cod increased at increasing level of applied data aggregation, while the fraction constituted by the other groups composed of lean prey decreased (Table 2.3). This could be explained by the change in prey composition of stomach content to which the evacuation model was applied when higher levels of data aggregation level was used: On haul level the evacuation rate of herring was low because fat, highenergy herring dominated the content of the stomachs from hauls in which it was present. In contrast, the evacuation rate of herring was significantly increased in the content of a 'quarterly mean stomach' representing the entire North Sea, for example, because the other prey types decreased the overall energy density of the content. The opposite trend applied to the prey group 'Other fish'. The results, thus, show that the composition of consumed prey is not necessarily the same as the composition found directly from the content of sampled stomachs. It should also be noticed that the differences observed here are absolute minimum values because food rations based on information on individual stomach are not included. In conclusion, it is recommended to apply the new evacuation model to data on individual stomach content whenever it is possible, or, alternatively, to exploit the lowest aggregation level of stomach data in cases where stomach contents have been pooled.

Table 2.2: New estimates of total food ration (g) for cod by age group and quarter of the year 1991, and associated coefficients of variation (CV) obtained by boot-strapping. Gastric evacuation model was applied to stomach content data at different levels of aggregation (haul, ICES square, round fish area, and total North Sea).

			Estir	mate						
		Sample	Square	Round	Total	Sample	Square	Round	Total	
quarte	r age								, 	
1	1	56	56	58	59	7	7	8	j 8	
	2	486	491	521	531	5	5	5	j 5	
	3	1470	1493	1584	1561	4	4	4	j 4	
	4	3363	3424	3800	3732	4	4	5	j 6	
	5	4611	4707	5251	5222	5	5	6	6	
	6	5351	5473	6081	6088	6	6	7	j 7	
2	1	130	131	134	134	4	4	4	5	
	2	1076	1091	1133	1134	3	3	3	3	
	3	2688	2715	2837	2863	3	3	3] 3	
	4	5663	5708	5989	6147	4	4	4	4	
	5	8707	8785	9247	9509	6	6	6	6	
	6	11989	12040	12766	13099	8	9	9	j 9	
3	0	23	23	24	23	19	19	18	16	
	1	317	320	331	337	5	5	5	5	
	2	1315	1320	1313	1287	4	4	4	4	
	3	2466	2480	2409	2292	4	4	4	4	
	4	4536	4536	4271	4187	6	6	6	6	
	5	5351	5358	4778	4840	9	9	10	9	
	6	8360	8364	8025	8497	19	19	19	18	
4	0	70	70	72	73	15	15	15	15	
	1	466	472	477	483	5	5	5	6	
	2	1812	1824	1835	1854	4	4	5	5	
	3	3733	3747	3769	3757	5	5	5	6	
	4	5741	5755	5824	5777	7	7	7	7	
	5	11031	11033	11546	11446	15	15	15	13	
	6	14366	14366	15187	15042	20	20	20	18	

With the exception of haddock, the new total quarterly food rations for 1991 differed generally from the old ones used at present by ICES (Figure 2.3). The new rations for whiting amounted to between one third and one half of the old food rations. The new estimates obtained for saithe were on the whole substantially lower than the old figures. The exception was quarter 2 of the year, where the new estimates were higher than the old ones. The new whiting and saithe estimates have been validated by bioenergetics studies performed by Andersen, Sand and Jordan (pers. comm.) and Andersen and Riis-Vestergaard (2005), respectively. Use of the old estimates implied that the fishes needed to swim at maximum sustained swimming speed most of their time which is highly unrealistic. The new rations obtained from cod increased at a faster rate with increasing predator age as compared to the previous estimates. This difference is probably rooted in the use of different temperature coefficients as well as powers relating evacuation rate to predator size.

Table 2.3: New estimates of food ration (g) by prey group for cod by age groups in quarter 3 of the year 1991. Gastric evacuation model was applied to stomach content data at different levels of aggregation (haul, ICES square, round fish area, and total North Sea.

Predator Cod, quarter 3

Predator Cod, quarter 3												
		age										
	3				4				5			
	Sample	Square	Round	Total	Sample	Square	Round	Total	Sample	Square	Round	Total
Group												
Ammodytidae	214	213	190	169	222	218	162	136	64	55	20	19
Annelida	168	159	89	79	199	198	93	80	106	106	84	84
Anomura mm	174	171	143	113	250	246	219	133	292	293	281	175
Astacidea	50	48	38	33	213	203	143	105	282	282	206	123
Caridea	11	11	7	6	35	35	23	16	42	42	24	23
Cephalopoda	9	4	5	6	36	12	18	21	0	0	0	0
Clupea harengus	276	302	486	577	1152	1238	1637	1939	1417	1458	1947	2288
Echinodermata	5	3	2	2	8	8	7	5	18	17	15	10
Euphausiacea	0	1	0	0	0	0	0	0	0	0	0	0
Gadus morhua	54	52	30	29	33	25	14	12	25	17	8	9
Limanda limanda	236	238	216	188	439	439	299	332	826	826	507	629
Melanogrammus aeglefinus	168	173	136	141	44	46	37	41	52	56	44	51
Merlangius merlangus	217	234	216	197	433	460	409	270	620	650	578	414
Other Crustaceans	0	0	0	0	1	1	0	0	2	2	0	0
Other Inv.	15	15	15	11	3	3	3	2	0	0	0	0
Other fish	403	395	319	265	794	765	608	509	1176	1130	803	716
Pleuronectes platess a				٠	•				•			
Solea solea	1	1	1	1	0	0	0	0				
Sprattus sprattus	47	48	71	56	20	21	24	14	6	6	9	7
Trisopterus esmarki	416	412	443	419	652	618	575	573	422	418	251	291
X Total	2466	2480	2409	2292	4536	4536	4271	4187	5351	5358	4778	4840

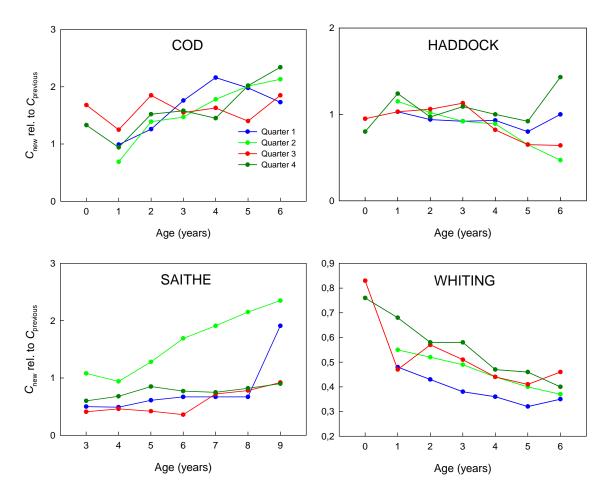


Figure 2.3: New estimates of total food ration by quarter of the year 1991 and predator age group expressed relative to old estimates for each gadoid predator.

The quarterly food rations for cod obtained from different years were quite similar (Figure 2.4). The estimated rations for haddock were also relative similar between years (Figure 2.5). With the exception of quarter 2, the values from 1991 were however a little lower than those estimated from 1981. The saithe rations from quarter 2 of 1991 were somewhat lower than those of 1981 (Figure 2.6). The difference may be explained by a lower condition factor for saithe in 1991 as indicated by a lower mean body mass at catch (ICES, 2005). Between-year estimates of food rations for whiting were similar except for quarter 1, were some differences occurred (Figure 2.7). None of the relatively few deviant quarterly rations were excluded, and smoothed estimates of total quarterly food rations by quarter of the year were provided for all four gadoids by application of GLM-model to estimates for all years (Figure 2.8).

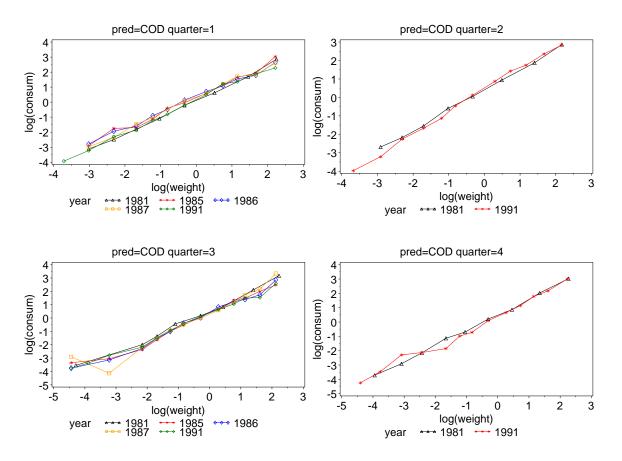


Figure 2.4: New estimates of total quarterly food ration (kg) for cod by year and body mass (kg) of the predator.

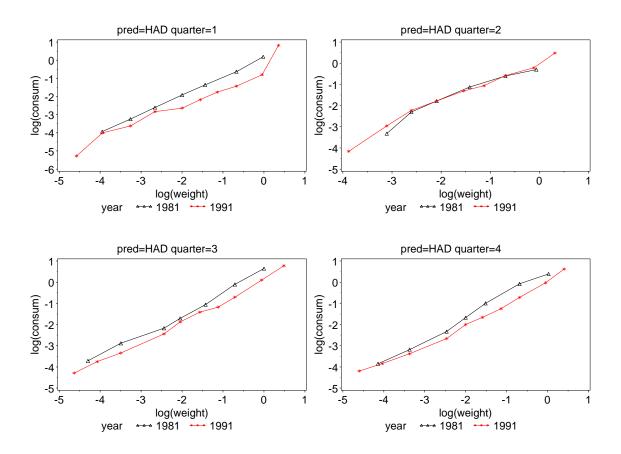


Figure 2.5: New estimates of total quarterly food ration (kg) for haddock by year and body mass (kg) of the predator.

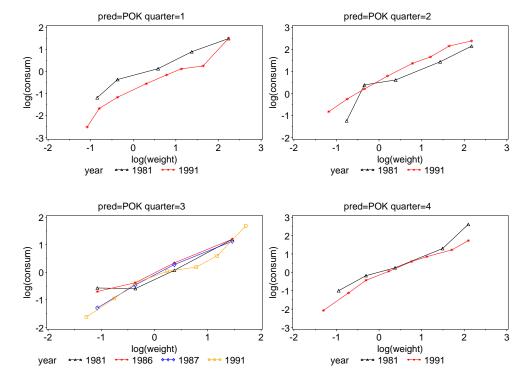


Figure 2.6: New estimates of total quarterly food ration (kg) for saithe (pollock) by year and body mass (kg) of the predator.

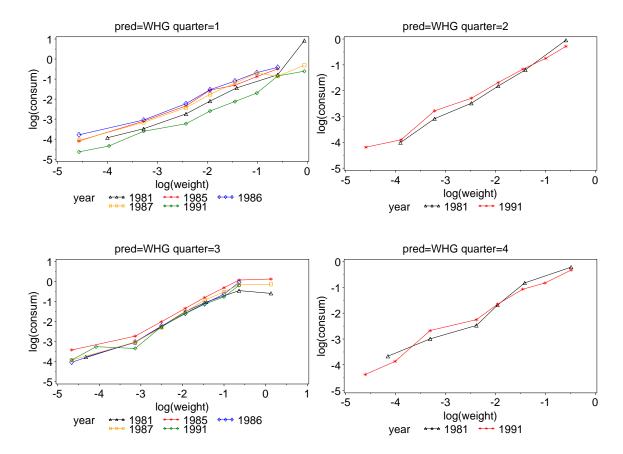


Figure 2.7: New estimates of total quarterly food ration (kg) for whiting by year and body mass (kg) of the predator.

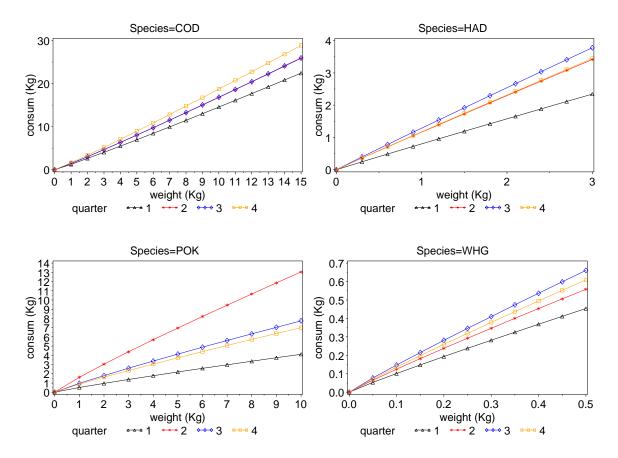


Figure 2.8: Total food ration (kg) for each gadoid predator by quarter of the year and predator body mass (kg) provided by application of GLM-model to estimates for all years (Figs. 2.5.2 – 2.5.5).

2.5.2 Ration estimates for mackerel

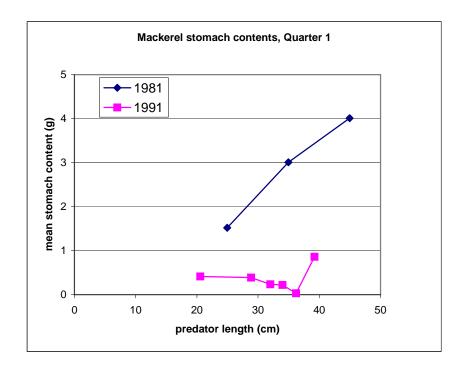
Until 1997 the estimates were based on a combination of a) the 1981 stomach content data b) gastric evacuation data referring to krill prey and c) a temperature effect of gastric evacuation taken from a mean of values estimated for other predators. The ambient temperatures applied to calculate the quarterly consumption rates were most likely those given in Daan (1986, *ICES Cooperative Research Report* on 1981 data). These temperature data were taken from an atlas of North Sea temperatures summarising data from 1900 –1950, taking into account the assumed distribution of mackerel in the North Sea. In 1997 results from new gastric evacuation experiments were available (documented in Temming *et al.*, 2002), as well as a new set of stomach content data from 1991. The new gastric experiments were performed with fish prey and revealed slower gastric evacuation rates and hence lower consumption rates. This effect was reinforced by the use of the 1991 stomach content data set, which was characterised by lower mean stomach contents, especially in quarters 1, 2 and 4. The effect on the model results was pronounced and concerns were expressed to use these new values in the key run, given the inherent uncertainties in the estimates. Therefore 1997 the previously used high consumption rates were used again.

In 2002 the decision was revised and the new estimates from 1997, based on the new evacuation rates and the 1991 stomach content values, were included in the key run. In addition a set of relatively low ambient temperature values was used: Q1: T=5.9, Q2: T=8.1, Q3: T=12.2 and Q4: T=9.5. These values reflect the assumption, that mackerel is mainly distributed in the North, were most of the commercial catch is taken. As an effect of the combined assumptions,

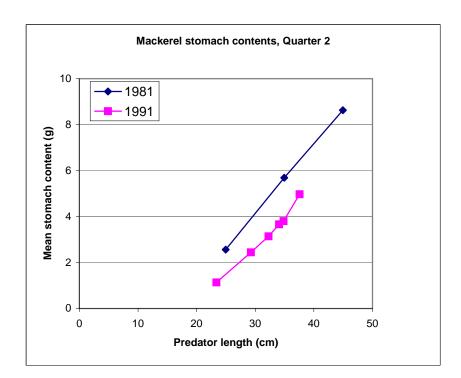
very low consumption rates and low impacts of the predator mackerel on its prey were predicted.

For the 2005 meeting additional information was available on gastric evacuation rates of invertebrate prey (krill) in mackerel (Temming *et al.*, 2002). These have been used to produce more realistic total prey consumption figures for mackerel, a species with only 25% fish in the diet. Calculated in this way, the consumption estimates can also be compared with those of other species, especially with horse mackerel (see below). If these figures, however, would be applied directly in MSVPA, the consumption of fish will be overestimated, due to the differences in evacuation rates between small invertebrates and fish and due to the fact that MSVPA can not handle differences in prey evacuation rates. Therefore the consumption figure was recalculated using the evacuation constants of fish only, as it was done in 1997 for the same reasons.

A comparison of the 1981 and the 1991 mean stomach contents revealed very low values for all quarters, especially for the first quarter. The reasons for this difference are unclear, but with the very low 1991 mean stomachs the total consumption values for mackerel are low in comparison to those of other predators, e.g., horse mackerel. It was therefore decided to recalculate the consumption estimates using the 1981 mean stomach content levels.

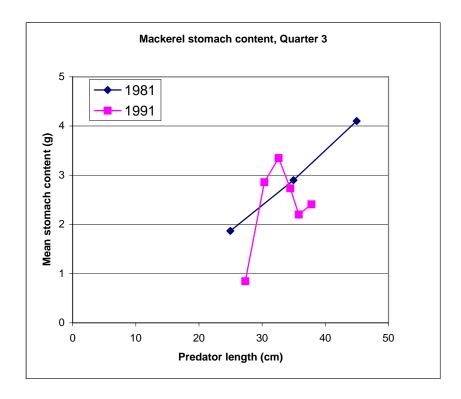


a)

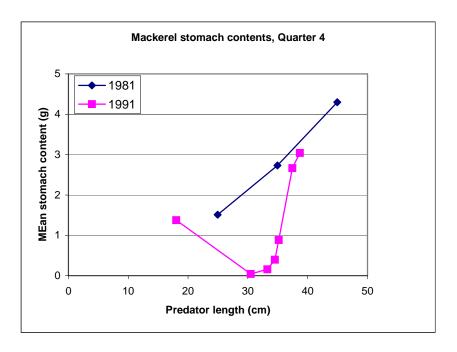


b)

Figure. 2.9 a-b. Mean stomach contents of mackerel from 1981 and 1991 by quarter. The mean values include empty stomachs.



c)



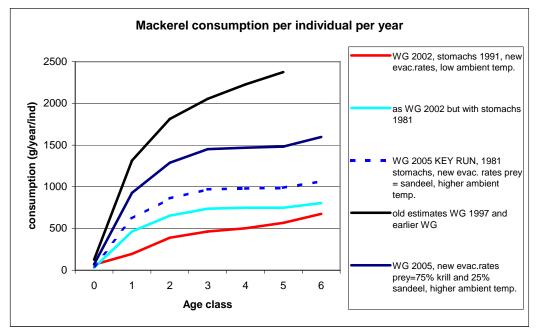
d)

Figure 2.9 continued: c-d. Mean stomach contents of mackerel from 1981 and 1991 by quarter. The mean values include empty stomachs.

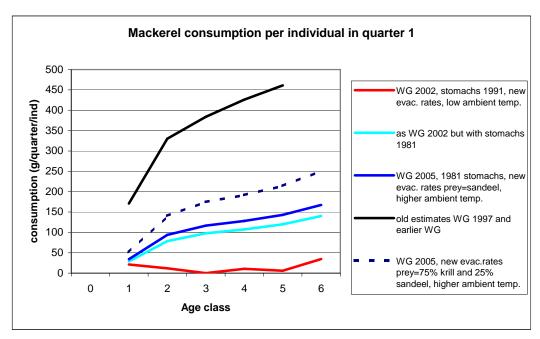
An analysis of the trawl survey data bases (IBTS, EGFS, SGFS) revealed high concentrations of mackerel in the southern and central North Sea. These are not reflected in the commercial catch data, which originate mainly from the Northern North Sea. This finding questions the low ambient temperatures used in 2002. As an alternative the quarterly ambient temperatures were recalculated using the model out from the HAMSOM hydrodynamic model for the years

1991 – 2001. A mean temperature was calculated including all ICES squares with non zero mackerel catches. No weighting by catch rates was applied, because in the deeper Northern regions the catchability of the GOV for mackerel is strongly decreasing. The new set of ambient temperatures is: Q1: $T=7.14^{\circ}C$, Q2: $T=8.84^{\circ}C$, Q3: $T=14.53^{\circ}C$ and Q4: $T=12.5^{\circ}C$.

For the key run in 2005 we applied consumption estimates that were based on the revised (higher) ambient temperatures, the 1981 mean stomach content data (higher than the 1991 data used in 2002) and evacuation parameters referring to lean fish (sandeel, values similar to those used in 2002). The effect of the different changes is displayed in Figure 2.10 for the yearly values (sum of 4 quarters) and separately for quarter 1:



a)



b)

Figure 2.10 a-b. Total annual (a) and quarter 1 (b) consumption of mackerel calculated with different stomach and experimental data sets and ambient temperatures.

2.5.3 Ration estimates for horse mackerel

The ration estimates for horse mackerel were for the first time changed in 1997, however based on a very limited set of experimental data. All experiments were carried out with lean fish prey. A single stomach data set was and is available sampled in 1991. Ambient temperatures for the horse mackerel were derived in 1997 from the temperature measurements conducted during the 1991 IBTS. A mean was calculated using catch rates of horse mackerel as weights. The values for the four quarters were Q1: T=6.4°C, Q2: T=9.59°C, Q3: T=17.75°C and Q4: T=13.73. The yearly consumption per size group calculated from these data sources

are displayed in Figure 2.11 (dashed red line). For the 2005 meeting the complete experimental results from gastric evacuation experiments were available (Temming and Herrmann 2001a, b). These experiments covered both lean fish and various invertebrate prey. Based on these data and the previously used 1991 stomach content data revised consumption rates were calculated (see Figure 2.11, solid red line). The differences in the yearly values were moderate, individual quarters differed more, because mainly the temperature effect was revised with the additional data.

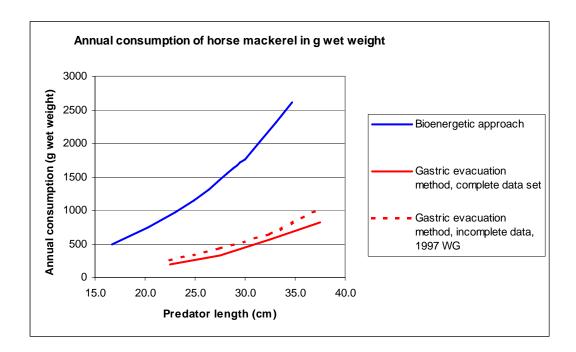


Figure 2.11. Annual consumption estimates of horse mackerel estimated with two different approaches.

The consumption estimates derived from stomach contents appear to be quite low, if compared to other species. To cross check this finding a complete bioenergetic budget was set up in the frame of the EU project CORMA (source CORMA report). Routine, standard and feeding metabolic rates were measured using intermitted flow respirometry (Herrmann and Enders, 2000 and CORMA report). Growth conversion efficiencies were estimated performing growth feeding trials in captivity. These data were combined with growth from field studies and measurements of energy density and of horse mackerel in different seasons. Energy cost for egg production were estimated based on published information. The cost for activity were assumed to be twice the standard metabolic rate (CORMA report). Integrating these data reveals an alternative estimate of the total quarterly and annual food intake, back transformed into wet weight units (Figures 2.11 and 2.12).

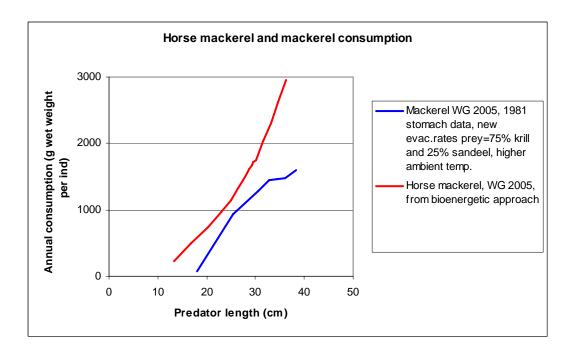


Figure 2.12. Comparison of horse mackerel and mackerel annual consumption rates in wet weight units. Note that the horse mackerel figure is based on a bioenergetic budget, while the estimates for mackerel were derived from stomach content data.

The estimates from the bioenergetic approach are considerably higher than those from stomach contents and gastric evacuation rates. This deviation is most likely due to problems in the stomach samples from 1991. The mean stomach content values appear to very low, if compared with those of mackerel. An example is shown for the third quarter (Figure 2.13). For comparison the results from a limited sampling in 1986 by Dahl and Kirkegard (1987) of horse mackerel stomachs are also included. In particular for the numerically important size class 30–35cm the mean stomach content in 1991 was only half of that observed in 1986 and only a third of that found for mackerel in 1991.

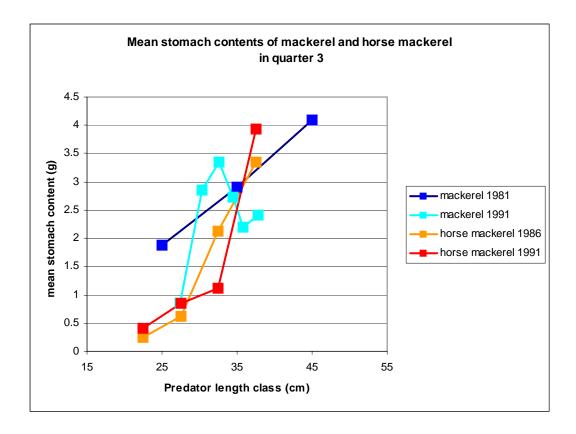


Figure 2.13: Comparison of mean stomach content values of mackerel and horse mackerel from quarter 3 in different years.

The low stomach contents may in part be related an under representation of copepod prey due to very high evacuation rates. The evacuation rates of copepods have so far not been investigated in comparison to those of larger invertebrate prey such as krill. The effect can be enforced, if a pronounced diel pattern in food intake exists (Dahl and Kirkegard, 1987), which is not adequately resolved with the sampling times.

The bioenergetic budget is on the other hand strongly influence by the assumption of activity costs being twice the standard metabolic rate. This implies that the costs do also increase strongly with ambient temperature. Depending on predator size and ambient temperatures the costs of activity in the total budget require 25 - 50% of the total consumption. The realism of an activity multiplier of two, however, was recently supported in an analysis of the bioenergetic budget for saithe (Andersen and Riis-Vestergaard, 2004).

Due to these considerations, the consumption rates based on the bioenergetic approach in horse mackerel were used in the key run. Like in the case of mackerel a modification was made to reduce the risk of an overestimation of the fish predation due to the inability of MSVPA to handle prey specific consumption rates. The bioenergetic budget in horse mackerel refers to a 70% share of small invertebrates in the diet, prey items which are definitely evacuated more rapidly than fish. In horse mackerel the fastest evacuation rate for krill was 1.35 times higher than that for herring (Temming and Herrmann 2001b). This factor and the ratio of fish to invertebrate prey (30:70) was used to decrease the consumption rates derived from the bioenergetic approach to yield the hypothetical consumption that would have been calculated from the same unknown stomach content using only the evacuation rates of fish. The actual stomach content is not needed to establish this correction, because it cancels out in the calculation. It is referred to as unknown, because the 1991 values are believed to be underestimated. The resulting correction factor is $0.8 \ (= R_{fish}/(0.70 * R_{krill} + 0.3 * R_{fish})$, with R being the respective gastric evacuation constants).

2.5.4 Marine mammals

Consumption values for grey seals have been updated by SMRU (University of St Andrews, UK). The new values are derived from the metabolic rate and activity schedules of grey seals. There remains the assumption that the seasonal diet of seals is still as it was when the original calorific values of the diet were calculated (Hammond *et al.* 1997).

	Consumption in kg per quarte				
	Previous values	New values			
quarter 1	654	654			
quarter 2	456	428			
quarter 3	440	352			
quarter 4	751	891			
total food per year per seal	2301	2325			
daily ration of food per seal in kilos	6.30	6.37			

3 Configuration of the North Sea key-run

3.1 Explorative runs

3.1.1 Inclusion of the 1981 mackerel diet data

The 1981 mackerel diet data were excluded from the key-run made in 1997 as described in section 2. The number of mackerel stomachs sampled in 1991 is quite limited and the additional diet information sampled in 1981 is advantageous. The effect of using the 1981 diet data was investigated by comparing a the results of a MSVPA using 1991 diet data only with a MSVPA using both the 1981 and 1991 diet data (the later key-run).

The differences in estimated predation mortality between the two runs are shown in Table 3.2 for the species Herring, Norway pout, sandeel and sprat. The effect was negligible for the remaining species.

One mackerel stomach included one sandeel in the stomachs sampled in first quarter of 1991. The remaining stomachs were practically empty. As result, it was estimated that 97% of the diet consisted of 1-group sandeel. In 1981, first quarter approximately 10% of the mackerel's diet consisted of sandeel. Significantly more stomachs were sampled in first quarter of 1981 compared to the numbers in 1991, such that the 1981 diet obtain a higher weight in the estimation of food suitabilities. The result is a much lower M2 on 1-group sandeel in the first quarter (Table 3.2) when the 1981 diet data are used.

The results of using the 1981 are a slight increase in sandeel M2 in the third quarter for the years where the North Sea mackerel was the dominant mackerel component in the North Sea. When the "Western mackerel" became dominant, the result of using the 1981 diet data is a relative lower sandeel M2.

For sprat, the predation mortality of the 0-group in the fourth quarter is much higher when the 1981 diet data are used (Table 3.2). This is mainly an effect of a relatively higher sprat proportion in the 1991 mackerel stomachs, especially for the "western stock" component.

In general, the mackerel diet estimated from the 1981 and 1991 stomachs samples are not that different. The very big North Sea component in the beginning of the assessment period and the following very big Western component in the most recent years do however result in quite large changes in predation mortalities for especially sandeel and sprat as an effect of using the two diet data set. For estimation of sandeel mortality the use of only the 1991 would be an error, as one sandeel found in one stomach cannot justify that 97% of the diet consist of sandeel. In the 2003 key-run, where only the 1991 mackerel data was used, the effect of this artefact was downscaled by choosing a food ration based on the very low observed stomach content. The first quarter mackerel ration was re-estimated this year based on data from both 1981 and 1991 and was in general 5 times higher than the rations used for the 2003 key-run. For consistency the use of 1981 and 1991 in both the estimation and diet seems therefore the most appropriate, even though the two diet data set were not compiled in exactly the same way.

3.1.2 Sensitivity of future cod stock development on grey gurnard abundance estimates

It was decided to exclude grey gurnard from the model in the keyrun 2003, since cod was predicted to go extinct in the forecast due to the predation pressure of grey gurnard on 0-group Intersessional work has revealed that this did not result from a model-artefact (Appendix 2) and it was then decided to re-include grey gurnard in the keyrun 2005. A sensitivity analysis was carried out to investigate the effect of a potential overestimation of grey gurnard stock numbers on future cod stock development.

Methodology

MSVPA runs were made where the grey gurnard stock were reduced by respectively 30, 50, 70 and 100 percent of the biomass used in the key-run. For each run Ricker stock-recruitment relations were fitted and later used in a 4M forecasts for the years 2004 to 2015. All forecasts used the 2003 level of fishing mortality and a stock size of "other predators" as observed for 2003.

Results

The predicted cod SSB was not much affected by the different reductions in grey gurnard stock numbers (Figure 3.1). For all levels of assumed gurnard biomass the cod stock showed a downward trend after 5–6 years where the SSB are independent of the initial population and are mainly determined by stock recruitments relations. Forecasts with a biomass of gurnards close to the key run gave the largest reduction in cod SSB.

Conclusions

At current fishing mortalities, the situation for cod is not much improved even with a substantial overestimation of grey gurnard. Once grey gurnard is included in the model, the different gurnard stock levels affect merely the rate of decline in cod SSB. A slight increase in cod SSB was only predicted when grey gurnard was excluded from the model, however this initial increase is later followed by a decline. Since a total exclusion of grey gurnard is not justified, the consistent downward trend in future cod SSB shows that grey gurnard is an important source for 0-group cod predation mortalities determining the future cod stock development. However, this analysis was based on the single available year of gurnard stomach data (1991), i.e., originating from a time period where predator and prey fields in the North Sea were sub-

stantially different from those in the late 1990s and more recent years. It is highly uncertain that the 1991 stomach data do reflect the most recent spatial-temporal overlap between grey gurnard and cod as well as the gurnard's diet. A more reliable investigation can however only be conducted when more recent grey gurnard stomach content data become available.

3.1.3 Effects of using updated sea-bird numbers.

The updated seabird numbers from WGSE were significantly higher than the numbers previously used. To see the effect of such increase, up to a factor five for some years, a MSVPA with the updated sea-bird numbers was made. It was not possible to compile the updated seabird diet data during the SG and the old diet set was used.

The new run gave unrealistic high partial predation mortality for some prey species. As an example, 45% of M2 on age-group 1 of cod in the first quarter was due to sea-birds in the new run. This seems very high, especially as the main bird predator was fulmar, which is known as being highly dependent on discards. It seems as if the discards had not properly been sorted out of the old bird diet data.

It was concluded that the new bird number estimate could not be used with the old diet data. The exercise showed however that the existing bird diet data probably need a revision.

3.2 Final configuration

Based on the results from the explorative runs, it was decided to configure MSVPA as presented in Table 3.1. These options are similar to previous year's options, with the exception of inclusion of grey gurnards.

The MSVPA key-run includes 10 fish species for which catch-at-age data are available (cod, whiting, saithe, haddock, herring, sprat, Norway pout, sandeel, plaice, and sole), and seven other predators for which stock size at age or length are available (grey seals, North Sea mackerel, Western mackerel, Starry ray (*Raja radiata*), sea birds, grey gurnards and horse mackerel).

Compared to the last key-run made (ICES 2003/D:09) the main difference in the basic configuration is the inclusion in grey gurnards as a predator, the use of 1981 mackerel diet data and a revision of the predator consumption rates as described in section 2.

The input data and their sources are as described in Section 2 of this report. Detailed input datasets are available at the ICES web server (www.ices.dk).

Table 3.1: Options used in MSVPA

VPA mode		= multispecies
Weight in stomach		= use weight in the
stomachs	a 1	
Plus group	Cod	= Yes, ICES age 0 - 11
Plus group	Whiting	= Yes, ICES age 0 - 8
Plus group	Saithe	= Yes, ICES age
0 - 10	11 1	
Plus group	Haddock	= Yes, ICES age 0 - 10
Plus group	Herring	= Yes, ICES age 0 -
9	G	T. T
Plus group	Sprat	= Yes, ICES age 0 - 4
Plus group	Norway pout	= no age 0 - 3
Plus group	Sandeel	= Yes, ICES age 0 - 4
Plus group	Plaice	= Yes, ICES age 0 - 10
Plus group	Sole	= Yes, ICES age 0 - 10
Food model		= constant other food
Consum model		= use fixed values
Include VPA species	Cod	= yes
Include VPA species	Whiting	= yes
Include VPA species	Saithe	= yes
Include VPA species	Haddock	= yes
Include VPA species	Herring	= yes
Include VPA species	Sprat	= yes
Include VPA species	Norway pout	= yes
Include VPA species	Sandeel	= yes
Include VPA species	Plaice	= yes
Include VPA species	Sole	= yes
Incl other predator	Grey Gurnards	= yes
Incl other predator	Grey Seals	= yes
Incl other predator	NS. Mackerel	= yes
Incl other predator	Other species	= no
Incl other predator	Raja radiata	= yes
Incl other predator	Sea birds	= yes
Incl other predator	Horse Mackerel	=
-	West Mackerel	•
Incl other predator		= yes
Include as predator	Cod Whiting	= yes
Include as predator	_	= yes
Include as predator	Saithe	= yes
Include as predator	Haddock	= yes
Include as prey	Cod	= yes
Include as prey	Whiting	= yes
Include as prey	Saithe	= no
Include as prey	Haddock	= yes
Include as prey	Herring	= yes
Include as prey	Sprat	= yes
Include as prey	Norway pout	= yes
Include as prey	Sandeel	= yes
Include as prey	Plaice	= no
Include as prey	Sole	= no
First and last VPA year		= 1963 to 2003
Year range stomach content		= 1981 to 1996

Table 3.2: Difference in predation mortality by year, quarter and age estimated from runs using 1981 and 1991 mackerel diet data (R8191) and using only 1991 mackerel diet data (R91). The difference in M2 is calculated as (R8191-R91)/R8191*100.

Species Herring

Age	 	197	70			198	0			199	90			200	00	
	1 1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
0	+ _ -0	+ _ 0	+ -11 42	7 1	 _ -1	 _ 0-	 8-	8 1	+ _ -1	+ ا _ ا 0-	+ 7 5	-0 1	 	 _ -0	+ 14 2	-2
2	-0 -0	-0 -0 -0	42 -0 0	-0 -0	0	0	-1 0	-0 -0	0 0	0	-0 -0	-0 -0	0	-0 0 0	2 -1 -0	-1 -1
4	-0	-1	-0	-0	-0	0	0	-0	0	0	-0	-0	0	0	-0	-1
5 6	-0 -0	-1 _	-2 1	-1 0	-0 -0	0 _	-0 1	-0 0	0 -0	0 _	-0 0	-0 -0	0 -0	0	-1 0	-1 -0

Species Norway pout

Age		197	'0			198	0		 	199	0			200	0	
	1 1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
0 1 2 3	_ -1 0 0	 -2 0 0	-11 -5 0 -0	-14 14 2 0		_ -2 0 0	-3 -8 0 -1	-6 8 0	_ -1 -0 0	-2 0 0	1 -9 0 0	-10 23 0 -0	_ -1 -0 0	_ -2 0 0	3 -8 -0 -0	-8 17 -0 -1

Species Sandeel

Age	 	197	70			198	30			199	90		 	200	0	
	1 1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
0	 _	-	† 7	8	_	 _	-11	-1	 _	,	-14	-0	 _	 _	-10	1
1	-52	19	6	-6	-7	16	-11	-4	-25	11	-18	-2	-9	5	-17	1
2	3	12	6	5	3	2	-20	5	4	3	-42	6	4	2	-42	5
3	4	-2	5	-1	4	-12	-25	-1	5	-3	-37	0	5	1	-33	-0
4	3	-11	28	-0	3	-24	-25	-1	3	-16	-67	0	3	-8	-37	-0

Species Sprat

Age	 	197	70		 	198	80			199	90			200	00	
	1 1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
 0 1 2 3 4	_ 1 0 0	+ -7 -11 -38	18 25 21 22 -2	9 -17 -2 -27	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	+ -9 -12 -37 -119	20 3 1 -0	16 -11 -2 -20	 3 1 1 0	-5	6	-148 -148 -21 -2 -14	_ 3 1 1 0	-12 -12 -4 -16 -52	25 4 2 2 -1	-21 -1 -20

cod 40reductions (%) ...⊜... 30 ______₅₀ **-**€-- 70 30gurnard exluded SSB 20-10 2014 2004 2008 2010 2012 2006 2005 2007 2009 2011 2013 2015 year

Figure 3.1: Predicted cod SSB development until 2015 with different levels of grey gurnard biomass.

4 Results and discussion of the North Sea key-run

4.1 Key-run results

Detailed output datasets, as well as the input data, are available at the ICES web server (www.ices.dk). In this report, an output summary by species is given in Table 4.1 and data are visualized in Figure 4.1. Predation mortality (M2) is presented in Table 4.3 and natural mortality (M1+M2) in Figure 4.2. A summary of the biomass eaten, yield and stock biomasses are given in Table 4.2 and Figures 4.3 and 4.4. An overview of partial M2 calculated as mean values over the full assessment period 1963–2003 is presented in Table 4.4. The same data, but only for the period 1994–2003, are presented in Table 4.5.

A detailed description of the key-run results requires more time than available during the SG meeting. This report highlights just the main changes due to changes in model setup and revision of input data. The main difference between the 2003 and 2005 key-run results is due to the re-introduction of grey gurnard as a predator and changes in predator rations. Gurnard mainly affects the predation mortalities of 0-group cod and whiting. In the 2003 key-run the cod 0-group M2 was relatively stable at a level of 1.45 for all the years. The M2 in the 2005 key-run is at the same level in 1963 but increases afterwards to around 4.0 in 2003 (Figure 4.2). Whiting shows a similar pattern in M2 between the two key-runs.

In addition to the changes in 0-group mortality due to gurnards, the 1-group mortality of **cod** (Figure 4.1) is in general higher in the new key-run. This increase in mainly due to the larger rations used for cod in the 2005 key-run, which lead to a greater level of cod cannibalism and a higher number of 1-group cod.

For **haddock** the stock dynamic looks rather similar to the previous key run.

The effect of re-introducing gurnard is a distinct increase in 0-group predation mortality of **whiting** for the years with a high biomass of gurnard. In addition, the raised cod rations result in a higher 1-group mortality in this year's key-run.

The biomass of **herring** which is consumed by predators is approximately 50% higher in this year's key-run compared to the 2003 key-run. This leads to a slightly higher total stock and spawning stock biomass, and a higher recruitment.

The effect of higher mackerel rations is higher predation mortality on **sandeel** and therefore higher sandeel stock size. If just the 1991 mackerel diet data were used, (as opposed to using both the 1981 and 1991 diet data), the increase in M2 would have been even higher. The temporal trend in biomass of sandeel is quite similar in two key-runs.

For **sprat** and **Norway pout**, the 2003 and 2005 key run results are quite similar, however with a slight increase in predation mortality and stock sizes for both species in the 2005 keyrun.

4.2 Key-run discussion

The reliability of MSVPA results hinges on adequate knowledge of the processes, and adequate input data. In comparison to the single species assessments, the MSVPA adds the quantification of the predation process, thereby shifting the balance between processes assessed from external data, and those quantified within the model. In particular, the balance between fishery mortality F (assessed) and natural mortality M (assumed) is improved in a multispecies assessment, by quantifying a major component of M. In addition to the predator stocks assessed within the MSVPA itself, external data on the abundance of other major predators have been used, including birds, seals, mackerel and horse mackerel, rays and gurnards. However,

over the years, the abundance of assessed predator stocks and externally determined predator stocks have changed, as reflected in the time series of consumptions (in biomass Figure 4.3 and in numbers Figure 4.4). In the late 1970s, when the MSVPA and stomach sampling programmes were set-up, the impact of predators assessed within the MSVPA exceeded the impact of externally determined predators, while in the 1990s, the reverse was true. **As a consequence, the accuracy of the abundance data for the external predators is now critical for the current MSVPA assessment.** In general, the stock sizes of these external or "other predators" is poorly estimated within the present ICES assessments. In addition, the proportion of the stock that can be found in the North Sea area is very uncertain for a key predator like mackerel.

The single species assessment of the important predators cod and whiting have furthermore become much more uncertain in the most recent years due to uncertain catch data and changes in fishing practice. As MSVPA mainly uses the same data and methodology as the single species assessment, the stock sizes of the important predators cod and whiting becomes very uncertain in the MSVPA assessment as well.

To conclude, the MSVPA results have become more uncertain in the most recent years of varies reasons. There has been shift of dominance between the "traditional" MSVPA predators towards "other predators", for which rather uncertain stock abundances exists. Stomachs sampling has historically been focused on the "traditional" MSVPA predators and for some "other predators" the number of stomach samples is quite low. The predation mortality for the whole assessment period 1963–2003 is based on stomachs sampled in the years 1981–1991. This dataset might not reflect the diet and stock distributions today, and this might bias the estimation of predation mortality.

Table 4.1:MSVPA output summary.

Species Cod

Year			I			Spawning		l l
		Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
 	Mean F Ages	1.July	1.January	Yield	1.January	1.January	predators	causes
		(millions)	(millions)	('000' t)				
 1963	+ 0.456	2054	+ 206	99	330	153	+ 47	 53
 1964	0.465	2887	497	110		171	•	
1965	0.526		695	162		214		
 1966	0.492		971	196		243		
1967	0.589		1002	232		267		
1968	0.591	2093	360	279		277		
1969	0.552	7684	471	204		278	•	
1970	0.527	4327	1706	226		294		
1971	0.645	681	1505	320		291	•	
1972	0.809	1478	289	371		251	•	
1973	0.672	3461	641	251		226	•	
 1974	0.658	1652	406	202		236	•	
 1975	0.691	886	565	186		214	•	
1976	0.672	7597	264	196		184	•	
1977	0.692	1593	1055	192		158	•	
1978	0.768	3974	684	265		162	•	
1979	0.661	3066	755	239		167	•	
1980	0.759	1805	1429	265		181	•	
1981	0.736		618	311		202	•	
1982	0.849	2791	946	281		197	•	
1983	0.867	1880	420	247		152	•	
1984	0.815		706	208		130	•	
1985	0.797	2511	158	203		124	•	
1986	0.848		774	192		112	•	
1987	0.866	1110	294	192		100	•	
1988	0.866	914	197	176		94	•	
1989	0.919	923	293	122		86	•	
1990	0.689	1292	142	107		75	•	28
1991	0.815	1637	171	88		76	•	
1992	0.657	1710		88	202		•	
1993	0.770		•				•	
' 1994	0.684		•	113			•	
1995	0.699			187			•	
1996	0.955			164				
1997	0.813			127				
1998	0.777			128			•	
1999	1.127			111				
2000	1.102			78				
2001	0.882			61				
2002	0.736			47			•	
2003	0.907			54		41	•	
Avg.	0.742			181			•	

Table 4.1: MSVPA output summary (Cont'd).

Species Haddock

Year						Spawning		
		Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
	Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
	Ages		+	+	+	+	+	+
	2 to 6	(millions)	(millions)	('000' t)	('000' t)	('000' t)	('000' t)	('000' t)
 1963	0.713	+ 899	+ 13096	274	+ 1098	110	+ 469	+ 156
1964	0.883	•		420			•	•
1965	0.814	•		368				•
1966	0.867			458				
1967	0.813			291				
1968	0.513							
1969	1.102							
1970	1.072							
1971	0.746							
1972	1.033							
1973	0.877	•		1		'	•	•
1974	0.842	•					•	
1975	1.017	•						
1976	1.043	'	'			•	•	
1977	1.042							
1978	1.055						•	'
1979	1.048	•		1				'
1980	0.964	'	'			'	•	
1981	0.708	'		221				'
1982	0.680							
1983	0.945			230				
1984	0.994							
1985	0.935							
1986	1.041	•		232				
1987	0.993		'	1	•	'		
1988	1.003							
1989	0.846							
1990	0.942							
1991	0.799	•		'	•	'	•	
1992	•							
1993	•				•			
1994	•			1	•			
1995	•				•			
1996	•			'	•			
1997	•			'	•		•	
1998	0.719							
1999	0.920	•		1			•	
2000	1.055			1	•			
2001				'	•			
2002	•							
2003	0.203							
Avg.	0.863	26675	4976	272	863	283	584	116

Table 4.1: MSVPA output summary (Cont'd).

Species Herring

Year						Spawning		
l		Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
	Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
	Ages 2 to 6	(millions)	(millions)	('000' t)				
	+	++	·		+		+	
1963	0.191							
1964	0.292				:		•	
1965	0.597			1285		2173	•	
1966	0.536					1917		
1967	0.718			778		1485		
1968	1.204			857	:	1009		
1969	0.962				:	804		
1970	0.972				:	833		
1971	1.255				:	573		
1972	0.587			450		620	•	
1973	0.987					610	•	
1974	0.947				:	334	•	
1975	1.346			254		202	•	
1976	1.301			159		207		
1977	0.593		1154	39	:	116	•	
1978	0.040			11	119	94		
1979	0.049		2081	24	:	150		
1980	0.212		5804	59	:	199		
1981	0.293		6223	167	:	345		
1982	0.213		8625	231	:	413	•	
1983	0.298	29486	13216	313	759	582	388	99
1984	0.380	19828	11881	314	1076	825	440	127
1985	0.555		10853	548	:	1035		
1986	0.480	44191	21173	519	1448	1056	673	
1987	0.474		26930	729	:	1431		225
1988	0.469		14442	750	:	1875	882	
1989	0.474	23192	10559	752	1911	1632	608	195
1990	0.379		7874	600		1411	•	183
1991	0.430		7777	573		1136	•	146
1992							•	133
1993					968		•	131
1994					972		972	
1995					967		921	
1996					904		444	
1997					1007		•	
1998					1428		500	
1999					1387		573	
2000					1401		413	
2001					1885		557	225
2002	0.193	15433	19509	370	2126	1787	665	258
2003	0.240		7034		2447	1793	694	
Avg.	0.540	35783	11526	460	1219	983	664	136

Table 4.1: MSVPA output summary (Cont'd).

Species Norway pout

				 ı	 I		 I	 I
Year						Spawning		
		Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
 	Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
 	Ages			. (. 0 0 0)	(1 0 0 0 1 +)	L(10001 +)		. (. 0 0 0 1 - 5)
 	1 to 2 +	(millions)	(millions) 	('000' t) 	('000' t) +	('000' t) +	('000' t) +	('000' t)
 1963	0.408	112570	23340	137	476	289	673	112
1964	0.160	182494	35264	61	521	227	1068	138
1965	0.084	231860	59173	43	824	306	1453	177
1966	0.076	152387	78546	52	1112	444	1420	183
1967	0.300	234044	55006	182	991	538	1502	192
1968	1.001	518000	77433	451	1096	460	2694	295
1969	0.234	673773	153961	113	1767	391	3904	374
1970	0.401	490736	218855	237	2614	645	3642	367
1971	0.460	515615	197524	305	2288	658	3709	386
1972	0.649	262697	194323	444	2251	668	2993	305
1973	0.764	432695	77079	345	1301	631	2426	232
1974	1.981	249512	133032	721	1449	297	1734	226
1975	0.983	521838	93741	494	1126	351	2546	284
1976	0.906	290962	169973	429	1859	432	2531	263
1977	0.646	119483	103282	363	1332	451	1356	174
1978	0.729	180989	46268	231	815	423	1117	145
1979	1.026	231134	70760	330	882	289	1281	190
1980	1.072	137552	95351	521	1205	417	1340	198
1981	0.766	359426	43760	426	950	541	1627	196
1982	1.102	218951	118906	355	1295	275	1670	208
1983	1.016	160358	88728	445	1184	443	1236	192
1984	1.232	159399	71410	340	1068	477	1225	158
1985	1.218	141570	57976	217	832	337	1055	115
1986	1.082	190790	52126	176	656	210	1152	116
1987	0.919	51803	62869	146	700	169	795	83
1988	0.709	95701	14572	101	311	186	535	61
1989	0.931	101690	30307	161	357	99	607	76
1990	0.882	84101	30721	127	420	151	554	70
1991	1.080	150732	29157	152	424	178	729	96
1992	1.038	91058	58770	257	681	195	773	114
1993	0.746	70588	33113	173	597	315	643	80
1994	1.354	280639	22925	176	400	197	1034	141
1995	0.438	150080	120273	183	1172	178	1629	188
1996	0.379	224696	44946	122	922	533	1287	159
1997	0.530	117791	101649	129	1134	297	1452	167
1998	0.222	116692	39016	61	793	456	1026	108
1999	0.694	220916	37033	85	605	274	1120	129
2000	0.605	194041	86030	175	910	208	1428	186
2001	0.191	233459	75909	57	1081	435	1732	188
2002	0.352	146880	81193	74	1174	437	1569	128
2003	0.474	176268	36444	21	633	249	1016	93
Avg.	0.728	226243	78555	235	1029	360	1543	178

Table 4.1: MSVPA output summary (Cont'd).

Species Plaice

	Year	1					Spawning		
		i i	Recruits	Recruits		Stock	Stock	Eaten by	Dead by
Ages		İ	Age 0	Age 1		Biomass	Biomass	model	other
2 to 10 (millions) (millions) ("000" t) ("000" to total total total total total total total total total total total total total total total		Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
		Ages		+	+	+	+	+	+
1964 0.344 327 964 117 564 310 0 45 1965 0.324 314 311 106 530 288 0 44 1966 0.320 286 298 106 548 307 0 45 1967 0.306 248 272 112 547 344 0 44 1968 0.270 333 235 120 511 350 0 41 1968 0.270 333 235 120 511 350 0 41 1968 0.290 336 317 330 317 330 489 337 0 33 1970 0.386 279 361 146 467 317 0 35 1971 0.340 234 266 111 450 296 0 35 1972 0.367 555 223 113 444 299 0 34 1973 0.409 467 528 117 443 269 0 34 1974 0.416 342 444 101 427 245 0 33 1975 0.433 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.409 439 460 112 446 257 0 34 1978 0.409 439 460 112 446 257 0 34 1978 0.409 439 460 112 446 257 0 34 1978 0.409 439 460 112 446 257 0 34 1978 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 33 1980 0.484 436 651 125 468 239 0 35 1980 0.484 436 651 125 468 239 0 35 1980 0.484 436 651 125 468 239 0 35 1980 0.496 500 509 500 509 500 5		2 to 10	(millions)	(millions)	('000' t)				
1965 0.324 314 311 106 530 288 0 444 1966 0.330 286 298 106 548 307 0 455 1966 0.330 286 298 106 548 307 0 455 1968 0.270 333 235 120 511 350 0 411 1969 0.290 380 317 130 489 337 0 339 1970 1970 0.340 234 266 111 450 296 0 355 1972 0.367 555 223 113 444 299 0 345 1972 0.367 555 223 113 444 299 0 345 1973 0.409 467 528 117 443 269 0 345 1973 0.409 467 528 117 443 269 0 345 1975 0.363 332 325 93 440 248 0 355 1975 0.432 332 325 93 440 248 0 355 1976 0.383 484 316 103 423 242 0 335 1976 0.383 484 316 103 423 242 0 335 1977 0.409 439 460 112 446 257 0 348 1979 0.560 684 433 138 448 256 0 335 1981 0.401 455 418 108 442 254 0 349 1982 0.507 610 1017 141 539 235 0 341 1982 0.507 610 1017 141 539 235 0 412 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.496 550 599 156 551 243 0 42 1986 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 60 617 584 299 0 35 1990 0.559 388 333 398 399 373 398 0 319	1963	0.337	1014	316	109	485	320	0	 39
1966	1964	0.344	327	964	117	564	310	0	45
1967 0.306 248 272 112 547 344 0 444 1968 0.270 333 235 120 511 350 0 41 1968 0.270 333 235 120 511 350 0 41 1969 0.290 380 317 130 489 337 0 339 1970 0.386 279 361 146 467 317 0 355 1971 0.340 234 266 111 450 296 0 35 1972 0.367 555 223 113 444 299 0 34 1973 0.409 467 528 117 443 269 0 34 1974 0.416 342 444 101 427 245 0 33 1975 0.432 332 325 93 440 248 0 35 1976 0.383 484 316 103 423 422 0 33 1977 0.409 439 460 112 446 257 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 259 235 0 41 1983 0.496 550 599 156 551 243 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 550 599 156 551 243 0 42 1985 0.496 550 599 156 551 243 0 42 1987 0.555 487 558 538 158 638 285 0 41 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1998 0.535 427 559 160 617 584 226 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1997 0.568 288 239 238 112 325 233 0 23 1995 0.538 251 277 119 375 219 0 28 1997 0.668 290 769 85 323 135 0 225 238 112 325 233 0 23 23 230 23 23 2	1965	0.324	314	311	106	530	288	0	44
1968	1966	0.330	286	298	106	548	307	0	45
1969	1967	0.306	248	272	112	547	344	0	44
1970 0.386 279 361 146 467 317 0 355 1971 0.340 234 266 111 450 296 0 355 1972 0.367 555 223 117 443 269 0 34 1973 0.409 467 528 117 443 269 0 34 1974 0.416 342 444 101 427 245 0 33 1975 0.432 332 325 93 440 248 0 33 1976 0.383 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 39 158 </td <td>1968</td> <td>0.270</td> <td>333</td> <td>235</td> <td>120</td> <td>511</td> <td>350</td> <td>0</td> <td> 41</td>	1968	0.270	333	235	120	511	350	0	41
1971 0.340 234 266 111 450 296 0 35 1972 0.367 555 223 113 444 299 0 34 1973 0.409 467 528 117 443 269 0 34 1974 0.416 342 444 101 427 245 0 33 1975 0.432 332 325 93 440 248 0 35 1976 0.383 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1981 0.481 1069	1969	0.290	380	317	130	489	337	0	39
1972 0.367	1970	0.386	279	361	146	467	317	0	35
1973 0.409 467 528 117 443 269 0 34 1974 0.416 342 444 101 427 245 0 33 1975 0.432 332 325 93 440 248 0 35 1976 0.383 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.552 888 313 98 299 182 0 22 1995 0.503 268 313 98 299 182 0 22 1996 0.582 888 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1999 0.574 324 276 74 334 336 165 0 27	1971	0.340	234	266	111	450	296	0	35
1974 0.416 342 444 101 427 245 0 33 1975 0.432 332 325 93 440 248 0 35 1976 0.383 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 42 1984	1972	0.367	555	223	113	444	299	0	34
1975 0.432 332 325 93 440 248 0 35 1976 0.383 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 42 1984 0.496 550 599 156 551 243 0 42 1985	1973	0.409	467	528	117	443	269	0	34
1976 0.383 484 316 103 423 242 0 33 1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1982 0.507 610 1017 141 539 235 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 <td>1974</td> <td>0.416</td> <td>342</td> <td>444</td> <td>101</td> <td>427</td> <td>245</td> <td>0</td> <td>33</td>	1974	0.416	342	444	101	427	245	0	33
1977 0.409 439 460 112 446 257 0 34 1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 26 1997 0.668 290 769 85 323 135 0 25 1999 0.574 324 270 84 336 165 0 27 2001 0.437 175 655 78 351 189 0 27 2002 0.437 175 655 78 351 189 0 25	1975	0.432	332	325	93	440	248	0	35
1978 0.401 455 418 108 442 254 0 34 1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2001 0.456 689 210 82 316 35 218 0 25 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25	1976	0.383	484	316	103	423	242	0	33
1979 0.560 684 433 138 448 256 0 33 1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 42 198	1977	0.409	439	460	112	446	257	0	34
1980 0.484 436 651 125 468 239 0 35 1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 44 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1997 0.668 290 769 85 323 135 0 25 1998 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25	1978	0.401	455	418	108	442	254	0	34
1981 0.481 1069 414 126 450 232 0 34 1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 339 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 389 0 25	1979	0.560	684	433	138	448	256	0	33
1982 0.507 610 1017 141 539 235 0 41 1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 24 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 25 2003 0.432 465 166 81 335 218 0 25	1980	0.484	436	651	125	468	239	0	35
1983 0.493 630 580 138 535 239 0 42 1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 25	1981	0.481	1069	414	126	450	232	0	34
1984 0.496 550 599 156 551 243 0 42 1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0	1982	0.507	610	1017	141	539	235	0	41
1985 0.496 1314 523 163 538 258 0 41 1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0	1983	0.493	630	580	138	535	239	0	42
1986 0.608 566 1250 165 650 274 0 50 1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.550 291 394 143 425 241 0 31 1992 0.590 291 394 143 425 241 0 31 1992 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0	1984	0.496	550	599	156	551	243	0	42
1987 0.559 588 538 158 638 285 0 50 1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0	1985	0.496	1314	523	163		258	0	41
1988 0.535 427 559 160 619 277 0 48 1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25	1986	0.608	566	1250	165	650	274	0	50
1989 0.472 420 406 177 584 296 0 44 1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0	1987	0.559	588	538	158	638	285	0	50
1990 0.439 413 399 173 533 298 0 41 1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 2000 0.395 221 308 83 320 179 0 <	1988						277	0	48
1991 0.552 415 393 168 470 269 0 35 1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 <t< td=""><td>1989</td><td>0.472</td><td>420</td><td>406</td><td>177</td><td>584</td><td>296</td><td>0</td><td>44</td></t<>	1989	0.472	420	406	177	584	296	0	44
1992 0.590 291 394 143 425 241 0 31 1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 <td< td=""><td>1990</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></td<>	1990								
1993 0.538 251 277 119 375 219 0 28 1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0									'
1994 0.535 329 238 112 325 203 0 23 1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25					•	'			
1995 0.503 268 313 98 299 182 0 22 1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25									
1996 0.582 808 255 86 268 157 0 20 1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25			•						
1997 0.668 290 769 85 323 135 0 25 1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25									
1998 0.556 284 276 74 334 161 0 27 1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25			•		•				
1999 0.574 324 270 84 336 165 0 27 2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25			•	'	•				
2000 0.395 221 308 83 320 179 0 25 2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25			•						
2001 0.456 689 210 82 316 207 0 24 2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25						'			
2002 0.437 175 655 78 351 189 0 27 2003 0.432 465 166 81 335 218 0 25			•						
2003 0.432 465 166 81 335 218 0 25									
	2002				•				
Avg. 0.456 464 438 120 456 252 0 35	2003								
	Avg.	0.456	464	438	120	456	252	0	35

Table 4.1: MSVPA output summary (Cont'd).

Species Saithe

Year						Spawning		
i i		Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
	Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
	Ages				+	+	++	
	3 to 6	(millions)	(millions)	('000' t)				
1963	0.332	159	194	24	178	98	0	36
1964	0.458	206	144	43	225	104	0	45
1965	0.468	165	186	56	275	85	0	55
1966	0.421	473	149	84	342	104	0	65
1967	0.323	440	428	81	387	133	0	77
1968	0.301	513	398	94	552	193	0	113
1969	0.256	258	464	114	731	248	0	149
1970	0.434	251	233	230	933	293	0	174
1971	0.335	265	227	264	1026	409	0	183
1972	0.403	302	240	298	891	458	0	151
1973	0.424	715	273	269	834	504	0	141
1974	0.585	218	647	283	840	508	0	139
1975	0.505	155	197	281	832	466	0	139
1976	0.801	140	140	378	722	298	0	114
1977	0.651	114	126	224	520	262	0	77
1978	0.483	295	104	144	428	227	0	68
1979	0.405	178	267	110	400	213	0	68
1980	0.460	212	161	115	412	222	0	68
1981	0.311	350	192	108	493	233	0	86
1982	0.499	527	316	155	505	189	0	86
1983	0.611	436	477	168	483	199	0	84
1984	0.815	170	394	211	501	152	0	91
1985	0.861	199	153	248	498	119	0	84
1986	0.959	107	180	227	441	111	0	75
1987	0.708	187	97	217	355	107	0	54
1988	0.666	218	169	150	276	111	0	44
1989	0.699	154	197	119	249	94	0	43
1990	0.621	241	139	104	266	84	0	48
1991	0.582	166	218	117	284	84	0	49
1992			151	108	296	91	0	53
1993	0.518	171	323	103	350	112	0	60
1994	0.511	261	155	100	362	109	0	65
1995	0.425	130	236	114	475	133	0	89
1996	0.424	222	117	110	471	155	0	
1997	0.296				468			87
1998	0.363			100	410	190	0	74
1999	0.372			107	434	213	0	74
2000	0.320			82	461			
2001				88	589			
2002								109
2003	'							
 Avg.	'			150				

Table 4.1: MSVPA output summary (Cont'd).

Species Sandeel

Year	 Mean F	Recruits Age 0 1.July	 Recruits Age 1 1.January	Yield	 Stock Biomass 1.January	Spawning Stock Biomass 1.January	 Eaten by model predators	Dead by other causes
	Ages 1 to 2	(millions)	(millions)	('000' t)	('000' t)	('000' t)	('000' t)	('000' t)
1963	0.177	1053869	++ 380357	162	2407	629	+ 2967	368
1964	0.123	1053213	379688	128	2363	609	2957	374
1965	0.120	720587	390442	130	2479	684	2710	361
1966	0.120	487287	268233	143	1954	751	1873	330
1967	0.180	980508	188574	188	1706	842	1929	364
1968	0.184	563482	360337	193	2559	761	2300	368
1969	0.112	326317	159452	113	1671	887	1357	274
1970	0.397	700739	94385	191	1229	796	1193	274
1971	0.313	357634	307245	188	1696	308	1405	311
1972	0.187	869190	151303	196	1722	994	1724	351
1973	0.134	762123	311715	168	2282	779	2332	367
1974	0.266	836531	164351	340	1735	991	1586	372
1975	0.307	608804	284865	359	2176	876	1917	388
1976	0.412	634111	146156	426	1579	922	1293	311
1977	0.485	680093	239385	588	1827	750	1347	365
1978	0.546	529924	329523	800	2266	779	1508	384
1979	0.479	734034	202924	684	2005	1083	1415	401
1980	0.600	349520	293202	724	2318	951	1514	343
1981	0.519	1018004	120988	528	1439	866	1537	292
1982	0.672	286313	357720	595	2119	533	1352	355
1983	0.493	797355	91277	530	1418	1008	1119	302
1984	0.406	321609	317152	750	2052	637	1239	327
1985	1.089	1174874	89158	707	1332	930	1400	282
1986	0.634	787738	438744	685	2365	374	1929	445
1987	0.478	377562	245915	791	2477	1351	1483	421
1988	0.859	966512	86791	1007	1710	1304	1375	273
1989	0.778	526304	293905	826	1827	455	1293	244
1990	0.913	792730	131372	584	1152	548	1197	202
1991	0.914	885715	218110	898	1356	383	1321	263
		487153						303
1993	0.419	766483	118331	576	1470	934	1269	307
		1002210		770	1783	797	1651	351
		569219		915	2122			381
1996		1775172			1710			
1997		540239			3530			
1998	0.613	662628	134228		2833			480
1999		806066			1893			
2000		977495			1646			
2001		1521247	274111	858	1845	587	2283	350
2002			402885		2441		1712	
	0.396				1256			
		762109			1938			

Table 4.1: MSVPA output summary (Cont'd).

Species Sole

	Year	<u> </u>					Spawning		
	i İ	i i	Recruits	Recruits		Stock		Eaten by	Dead by
Ages	i I	i i	Age 0	Age 1		Biomass	Biomass	model	other
2 to 8 (millions) (millions) ("000" t) ("000		Mean F	1.July	1.January	Yield	 1.January	1.January	predators	causes
1963 0.490 563 9 35 66 64 0 5 1964 0.327 127 536 15 67 38 0 5 1965 0.355 41 121 21 107 31 0 9 1966 0.329 78 39 38 106 88 0 8 1967 0.411 104 74 36 97 88 0 7 1968 0.444 52 99 35 92 77 0 6 1969 0.495 144 49 29 75 59 0 5 1970 0.392 43 137 20 66 52 0 5 1971 0.472 80 41 22 66 45 0 4 1972 0.407 113 76 18 58 49 0 4 1973 0.492 114 107 16 54 38 0 4 1974 0.489 42 109 16 58 38 0 4 1975 0.494 118 40 19 58 41 0 4 1977 0.409 49 139 16 57 35 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.489 160 149 14 53 26 0 3 1981 0.489 167 88 71 26 69 47 0 4 1983 0.594 85 71 26 69 47 0 4 1984 0.584 85 71 26 69 47 0 4 1986 0.572 75 59 17 56 31 0 4 1988 0.515 114 451 21 75 56 31 0 4 1988 0.515 14 451 21 75 56 31 0 4 1988 0.515 14 451 21 75 56 31 0 4 1988 0.515 14 451 21 75 56 31 0 4 1999 0.477 76 179 33 31 17 94 0 99 1991 0.500 60 69 31 107 59 0 8 1992 0.490 474 71 17 56 31 0 4 1998 0.552 53 96 30 75 62 0 5 1999 0.477 76 179 33 32 109 82 0 6 1999 0.477 76 179 33 31 17 94 0 99 1991 0.500 60 69 31 107 59 0 8 1992 0.492 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 87 23 66 44 0 5 1995 0.565 59 135 21 63 22 65 46 0 4 1997 0.606 142 269 15 51 31 31 0 5 1998 0.655 92 355 36 30 75 62		Ages		· 	+	+	+	+	
1964 0.327 127 536 15 67 38 0 5 1965 0.355 41 121 21 107 31 0 9 9 1966 0.329 78 39 38 106 88 0 88 1967 0.411 104 74 36 97 88 0 7 1968 0.444 52 99 35 92 77 0 6 1968 0.444 52 99 35 92 77 0 6 1969 0.495 144 49 29 75 59 0 5 1970 0.392 43 137 20 66 52 0 5 1971 0.472 80 41 22 66 45 0 4 1972 1971 0.472 80 41 22 66 45 0 4 1973 0.492 114 107 16 54 38 0 4 1973 0.492 114 107 16 54 38 0 4 1974 0.499 42 109 16 58 38 0 4 1975 0.494 118 40 112 15 54 43 0 4 1976 0.494 118 40 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 33 0 4 1978 0.521 12 47 19 60 33 0 4 1983 0 4 1983 0.498 158 11 19 54 47 0 33 0 4 1983 0.499 74 141 24 70 43 26 0 4 1983 0.499 74 141 24 70 43 26 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.549 167 81 23 58 45 0 47 0 4 1983 0.549 167 81 23 58 45 0 47 0 4 1986 0.549 167 81 23 58 45 0 47 0 4 1988 0.515 114 451 22 105 33 117 94 0 99 1991 0.504 371 72 35 110 83 0 8 1992 0.477 76 179 33 317 94 0 99 1991 0.504 371 72 35 110 83 0 8 1992 0.660 60 69 31 107 59 0 8 1994 0.553 101 57 33 32 109 82 0 44 1995 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 32 109 82 0 44 1997 0.666 142 269 15 51 31 0 34 34 30 34 34 30 34 34	 	2 to 8	(millions)	(millions)	('000' t)	('000' t) 	('000' t) 	('000' t) +	('000' t)
1965 0.355 41 121 21 107 31 0 9 1966 0.329 78 39 38 106 88 0 8 1967 0.411 104 74 36 97 88 0 7 1968 0.444 52 99 35 92 77 0 6 1969 0.495 144 49 29 75 59 0 5 1970 0.392 43 137 20 66 52 0 5 1971 0.472 80 41 22 66 45 0 4 1972 0.407 113 76 18 58 49 0 4 1973 0.492 114 107 16 54 38 0 4 1973 0.492 114 107 16 54 38 0 4 1975 0.494 118 40 19 58 41 0 4 1976 0.443 146 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1983 0.522 149 152 20 62 35 0 4 1983 0.594 85 71 26 69 47 0 4 1986 0.592 78 167 81 23 58 45 0 4 1988 0.594 85 71 26 69 47 0 4 1988 0.592 16 17 81 23 58 45 0 4 1989 0.490 474 71 17 56 31 0 4 1989 0.491 18 10 22 55 42 0 58 1991 0.594 85 71 27 35 110 83 0 8 1992 0.490 474 71 17 56 31 0 4 1989 0.417 18 10 22 56 46 0 8 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1994 0.553 101 57 33 117 94 0 99 0 1995 0.562 53 96 30 75 63 00 8 1997 0.606 142 269 15 51 51 31 0 4 1998 0.655 92 135 21 63 22 65 46 0 4 2001 0.685 75 149 22 65 66 44 0 5 2002 0.543 134 134 133 19 70 34 0 5	1963	0.490	563	9	35	66	64	0	5
1966	1964	0.327	127	536	15	67	38	0	5
1967 0.411 104 74 36 97 88 0 7 1968 0.444 52 99 35 92 77 0 66 1968 0.444 52 99 35 92 77 0 66 1969 0.495 144 49 29 75 59 0 5 59 1970 0.392 43 137 20 66 52 0 5 5 1971 0.472 80 41 22 66 45 0 4 1972 0.407 113 76 18 58 49 0 4 1973 0.492 114 107 16 54 38 0 4 1973 0.492 114 107 16 58 38 0 4 1974 0.489 42 109 16 58 38 0 4 1975 0.494 118 40 19 58 41 0 4 1976 0.494 118 40 19 58 41 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.521 12 47 19 60 39 0 4 1981 0.521 12 47 19 60 39 0 4 1981 0.489 160 149 14 53 26 0 4 1982 0.489 160 149 14 53 26 0 4 1982 0.524 149 152 20 62 35 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 43 0 5 1988 0.572 75 159 17 56 31 0 4 1988 0.572 75 159 17 56 31 0 4 1988 0.572 75 159 17 56 31 0 4 1988 0.572 75 159 17 56 31 0 4 1988 0.560 60 69 31 107 59 0 8 1992 0.490 474 71 17 56 31 0 4 1992 0.490 474 71 17 56 31 0 4 1992 0.490 474 71 17 56 31 10 31 30 31 31 31 31	1965	0.355	41	121	21	107	31	0	9
1968	1966	0.329	78	39	38	106	88	0	8
1969	1967	0.411	104	74	36	97	88	0	7
1970 0.392 43 137 20 66 52 0 5 5 1971 0.472 80 41 22 66 45 0 4 1972 0.407 113 76 18 58 49 0 4 4 1973 0.492 114 107 16 54 38 0 4 4 1974 0.489 42 109 16 58 38 38 0 4 4 1975 0.494 118 40 19 58 41 0 4 4 1977 0.409 49 139 16 57 35 0 4 4 1977 0.409 49 139 16 57 35 0 4 4 1978 0.521 12 47 19 60 39 0 4 4 1979 0.478 158 11 19 54 47 0 3 3 198 0 4 1982 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.584 85 71 26 69 47 0 4 1986 0.572 75 159 17 56 37 0 4 1986 0.572 75 159 17 56 37 0 4 1986 0.572 75 159 17 56 37 0 4 1988 0.515 114 451 21 75 42 0 58 1994 0.477 76 179 33 117 94 0 98 1994 0.553 101 57 35 101 37 99 0.477 76 179 33 117 99 0.477 76 179 33 117 99 0.477 76 179 33 117 99 0.477 76 179 33 117 99 0.477 76 179 33 117 99 0.552 101 37 0 8 1992 0.482 73 353 32 109 82 0 98 1994 0.553 101 57 33 32 109 82 0 98 1994 0.553 101 57 33 32 109 82 0 98 1994 0.553 101 57 33 32 109 82 0 98 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 44 0 5 1996 0.724 282 50 22 56 46 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 66 67 67 67 67 67 6	1968	0.444	52	99	35	92	77	0	6
1971 0.472 80 41 22 66 45 0 4	1969	0.495	144	49	29	75	59	0	5
1972 0.407 113 76 18 58 49 0 4 1973 0.492 114 107 16 54 38 0 4 1974 0.489 42 109 16 58 38 0 4 1975 0.494 118 40 19 58 41 0 4 1976 0.443 146 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152	1970	0.392	43	137	20	66	52	0	5
1973 0.492 114 107 16 54 38 0 4 1974 0.489 42 109 16 58 38 0 4 1975 0.494 118 40 19 58 41 0 4 1976 0.493 146 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.572 75 159 17 56 37 0 4 1988 0.515 114 451 21 75 42 0 5 1988 0.515 114 451 21 75 42 0 5 1988 0.515 114 451 21 75 42 0 5 1990 0.477 76 179 33 117 94 0 99 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 1	1971	0.472	80	41	22	66	45	0	4
1974 0.489 42 109 16 58 38 0 4 1975 0.494 118 40 19 58 41 0 4 1976 0.443 146 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1986 0.572 75 159 17 56 37 0 4 1988 0.515 114 451 21 75 42 0 5 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 6 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 60 44 0 5	1972	0.407	113	76	18	58	49	0	4
1975 0.494 118 40 19 58 41 0 4 1976 0.443 146 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 <t< td=""><td>1973</td><td>0.492</td><td>114</td><td>107</td><td>16</td><td>54</td><td>38</td><td>0 </td><td>4 </td></t<>	1973	0.492	114	107	16	54	38	0	4
1976 0.443 146 112 15 54 43 0 4 1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 <	1974	0.489	42	109	16	58	38	0	4
1977 0.409 49 139 16 57 35 0 4 1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1987 0.490 474 71 17 56 37 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1995 0.560 60 69 31 107 59 0 6 1995 0.544 282 50 22 56 42 0 5 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 42 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 140 231 18 63 42 0 4 2001 0.665 92	1975	0.494	118	40	19	58	41	0	4
1978 0.521 12 47 19 60 39 0 4 1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.560 60 69 31 107 59 0 8 1995 0.544 128 269 15 51 31 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.554 157 87 22 56 42 0 5 1999 0.544 157 87 23 66 44 0 5 1998 0.655 75 149 22 65 46 0 44 1997 0.606 142 269 15 51 31 0 3 1998 0.655 75 149 22 65 46 0 44 1997 0.606 142 269 15 51 31 66 44 0 5 1998 0	1976	0.443	146	112	15	54	43	0	4
1979 0.478 158 11 19 54 47 0 3 1980 0.456 157 150 13 46 36 0 3 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1985 0.549 167 81 23 58 45 0 4 1988 0.572 75 159 17 56 37 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 22 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 44 0 5 1999 0.544 157 87 23 66 46 0 44 10 5 10 10 10 10 10 10	1977	0.409	49	139	16	57	35	0	4
1980 0.456 157 150 13 46 36 0 3 1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417	1978	0.521	12	47	19	60	39	0	4
1981 0.489 160 149 14 53 26 0 4 1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 70 34 0 5	1979	0.478	158	11	19	54	47	0	3
1982 0.542 149 152 20 62 35 0 4 1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8	1980	0.456	157	150	13	46	36	0	3
1983 0.499 74 141 24 70 43 0 5 1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 6 1995 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.724 282 50 22 56 42 0 4 1999 0.544 157 87 23 66 44 0 5 1000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 70 34 0 5	1981	0.489	160	149	14	53	26	0	4
1984 0.584 85 71 26 69 47 0 4 1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 6	1982	0.542	149	152	20	62	35	0	4
1985 0.549 167 81 23 58 45 0 4 1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 <	1983	0.499	74	141	24	70	43	0	5
1986 0.572 75 159 17 56 37 0 4 1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5	1984	0.584	85	71	26	69	47	0	4
1987 0.490 474 71 17 56 31 0 4 1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1985	0.549	167	81	23	58	45	0	4
1988 0.515 114 451 21 75 42 0 5 1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1986	0.572	75	159	17	56	37	0	4
1989 0.417 188 108 22 101 37 0 8 1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5	1987	0.490	474	71	17	56	31	0	4
1990 0.477 76 179 33 117 94 0 9 1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 20	1988	0.515	114	451	21	75	42	0	5
1991 0.504 371 72 35 110 83 0 8 1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0	1989	0.417	188	108	22	101	37	0	8
1992 0.482 73 353 32 109 82 0 8 1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002	1990	0.477	76	179	33	117	94	0	9
1993 0.560 60 69 31 107 59 0 8 1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1991	0.504	371	72	35	110	83	0	8
1994 0.553 101 57 33 91 79 0 6 1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1992	0.482	73	353	32	109	82	0	8
1995 0.562 53 96 30 75 63 0 5 1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1993	0.560	60	69	31	107	59	0	8
1996 0.724 282 50 22 56 42 0 4 1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1994	0.553	101	57	33	91	79	0	6
1997 0.606 142 269 15 51 31 0 3 1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1995	0.562	53	96	30	75	63	0	5
1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1996	0.724	282	50	22	56	42	0	4
1998 0.655 92 135 21 63 22 0 5 1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1997	0.606	142	269	15	51	31	0	
1999 0.544 157 87 23 66 44 0 5 2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1998	0.655	92	135	21	63	22	0	
2000 0.615 75 149 22 65 46 0 4 2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	1999								
2001 0.489 243 71 20 60 37 0 4 2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	2000							0	
2002 0.547 140 231 18 63 42 0 4 2003 0.434 134 133 19 70 34 0 5	2001	0.489	243	71	20	60	37	0	
2003 0.434 134 133 19 70 34 0 5	2002	0.547	140	231	18	63	42	0	
	2003	0.434	134	133	19	70	34	0	
	Avg.	0.495	137	128	23	72	49	0	5

Table 4.1: MSVPA output summary (Cont'd).

Species Sprat

Year						Spawning		
İ	i I	Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
	Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
	Ages				+	+	+	
 	1 to 2 +	(millions)	(millions)	('000' t)	('000' t) 	('000' t)	('000' t) +	('000' t)
1963	0.087	341713	160654	67	1144	881	1000	214
1964	0.085	244116	165866	70	1162	902	903	216
1965	0.090	336512	123213	76	1144	947	892	212
1966	0.141	397388	172477	107	1222	950	960	242
1967	0.062	322955	201900	71	1377	1049	1029	265
1968	0.064	228059	169466	71	1608	1308	1094	241
1969	0.058	160474	102090	69	1241	1078	710	189
1970	0.054	249376	70618	62	937	824	479	176
1971	0.078	279764	130821	86	1106	902	582	230
1972	0.077	551855	144432	108	1364	1126	1014	290
1973	0.151	631993	299374	261	2027	1519	1366	378
1974	0.150	313433	324995	278	2257	1751	1166	453
1975	0.315	571305	167375	568	2569	2298	1288	453
1976	0.361	304000	314921	527	2443	1939	1148	406
1977	0.236	283139	149570	283	1820	1576	1016	294
1978	0.455	420866	141635	400	1654	1418	952	262
1979	0.583	236646	209022	412	1316	961	758	183
1980	0.753	191606	116512	305	1063	857	626	112
1981	0.822	71501	78862	180	632	489	311	59
1982	0.903	39226	33032	139	338	284	133	34
1983	0.929	121281	15535	82	158	133	123	32
1984	0.650	35475	58184	78	237	145	144	47
1985	0.257	32121	13664	49	246	224	138	42
1986	0.126	103997	14562	15	218	194	159	43
1987	0.912	161327	38277	44	205	142	271	42
1988	0.782	200305	20533	82	217	182	298	39
1989	0.942	135101	41625	63	231	160	258	37
1990	0.204	82741	24374	41	204	162	176	34
1991	0.334	135999	29032	69	230	184	204	50
1992	0.364	210105	50611	103	293	214	304	69
1993	0.496	396179	61028	180	429	331	494	106
1994	0.469	156703	156596	323	756	511	447	143
1995	0.739	62421	58048	357	709	620	320	109
1996					463		158	53
1997	0.358	109189	33462	100	230	180	176	
1998	0.589	149860	40067	162	293	232	246	
1999	0.504	116696	58821	188	385			
2000	0.568	66047	47222	195	404		179	
2001	1.424			211	306		148	
2002	0.784	141167	39736	146	189		200	
2003			52249				191	
Avg.					856		544	

Table 4.1: MSVPA output summary (Cont'd).

Species Whiting

Year						Spawning		
		Recruits	Recruits		Stock	Stock	Eaten by	Dead by
		Age 0	Age 1		Biomass	Biomass	model	other
	Mean F	1.July	1.January	Yield	1.January	1.January	predators	causes
 	Ages 2 to 6	 (millions)	(millions)	('000' t)	+ ('000' t)	('000' t)	 ('000' t)	('000' t)
+	+	·	+		+	+	+	
1963	0.861	8687	7287	233	703	378	280	103
1964	0.548	15189	1979	141	670	554	286	106
1965	0.527	14762	4457	176	767	561	337	107
1966	0.980	19619	4293	242	696	485	348	88
1967	0.695	30792	7035	207	699	364	428	100
1968	0.773	10675	13962	237	1085	457	553	143
1969	0.555	13045	1734	319	898	771	364	113
1970	0.689	12055	2691	286	647	524	240	75
1971	0.443	19680	4232	174	456	263	246	70
1972	0.655	30363	8439	208	715	325	465	105
1973	0.846	25890	11720	286	1055	501	706	127
1974	0.959	21183	4049	323	777	570	360	102
1975	1.086	24674	7711	276	783	448	424	117
1976	0.930	38131	6565	326	911	592	622	117
1977	0.728	23379	5486	289	836	576	383	116
1978	0.659	38715	7439	205	854	492	616	121
1979	0.635	24536	7597	249	966	596	480	125
1980	0.794	29940	8105	235	1000	607	574	134
1981	0.735	30214	5922	202	1027	670	662	109
1982	0.591	13885	2977	140	643	493	312	81
1983	0.675	10818	2351	167	492	376	196	65
1984	0.867	27856	3834	147	462	280	419	65
1985	0.727	16749	2655	100	385	255	244	60
1986	0.842	22266	5046	168	515	283	368	77
1987	1.069	20584	4260	161	528	323	336	77
1988	0.818	20990	3214	181	511	348	302	76
1989	0.914	24314	5718	153	570	306	412	84
1990	0.837	18831	3199	204	534	364	319	73
1991	0.617	12964	2250	145	412	305	203	60
1992	0.575	24515	2342	121	396	285	317	63
1993	0.670	21618	3332	109	438	279	325	65
1994	0.646	24660	3480	86	455	283	402	67
1995	0.532	41240	3149	97	453	300	552	74
1996	0.472	11199	2463	68	429	302	266	57
1997	0.333	34611	1345	53	325		457	
1998			2493	39	345		719	
1999			4919	54	479	219	837	
2000			2879	57	353	217	480	
2001			2746	43			462	
2002							432	
2003			818		392		163	
 Avg.			4598				412	

Table 4.2: MSVPA results, System summary.

Year	1775-	VPA						
	VPA	species		Average	VPA		Total	VPA
	species	Spawning		stock		Other food		
	Stock	Stock	VPA		Eaten by		on by	Dead by
	Biomass	Biomass	species	other	model	model	model	other
	1.Jan	1.jan	Yield	predators 	predators 	predators	predators 	causes
	('000' t)	('000' t)	('000' t)	('000' t)	('000' t)	('000' t)	('000' t)	('000' t)
1963	8263	4650	1740	3204	6977	9538	16515	1389
1964	8662	5153	1992	2983	7093	8788	15882	1469
1965	8960	5259	2428	2734	7438	8206	15645	1460
1966	8394	5108	2337	2411	6539	8809	15349	1392
1967	7784	4714	2182	2162	7983	11773	19756	1529
1968	10499	4461	2654	1580	9439	10035	19474	1800
1969	9609	5026	2726	1467	8008	9484	17492	1701
1970	8660	4904						•
1971	8682	3664			1	1	1	1
1972	9037	4454					•	
1973	8638	4612	2513		1	1	1	!
1974	8331	4639						1
1975	8711	4652	3055		1	1	14588	1674
1976	8077	4427	2993				•	1
1977	6703	3773			1	1	1	1
1978	6460	3439					•	
1979	6204	3309			1	!	1	!
1980	6881	3243	2595					1
1981	5643	3204	2287		1	1	•	1
1982	6263	2557	2277				•	1043
1983	5342	3048			1		1	
1984	6183						•	
1985	5424	3139	2508		1	1	1	!
1986	6210	2517	2401				•	1
1987	6840	3675	2629		1	1	1	1065
1988	5859	4051	2825				•	1
1989	5525	2982			1			•
1990	4581	2955	2063			1	1	719
1991	4424	2469			1	!	1	!
1992	4897	2387	2377					1
1993	4801	2751	2114				•	!
1994	5109	2808	2334				•	•
1995	6309	2858	2657					
1996	5208	3180	1904				1	1
1997	6964	2540	2077		1	!	13005	1308
1998	6431	4382					12230	1
1999	5339	3360	1814		1	1	14089	962
2000	5743	2861	1817				•	1
2001	6573	3474			1		1	
2001	7405	3963	1817			1	1	1178
2002	6205	4331	1374	!	!	7563	1	!
Mean	6203 6874	3701	2346					1206
rican	00/4	3/01	2340	1432	1 5550	/014	1 13345	1200

Table 4.3: Predation mortality (M2).

Species Cod

Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
0	1.319	1.324	1.315	1.228	0.965	1.391	1.405	0.956	0.757	0.736	2.041
1	0.528	0.654	0.827	0.929	1.091	0.858	0.990	1.132	0.924	0.830	1.027
2	0.276	0.309	0.420	0.491	0.534	0.413	0.527	0.661	0.504	0.395	0.513
3	0.106	0.127	0.148	0.161	0.181	0.149	0.189	0.217	0.174	0.140	0.183
4	0.019	0.020	0.020	0.021	0.023	0.020	0.025	0.028	0.026	0.021	0.024
5	0.013	0.012	0.011	0.010	0.010	0.011	0.012	0.012	0.012	0.011	0.013
6	0.026	0.025	0.023	0.022	0.020	0.022	0.024	0.024	0.025	0.023	0.026
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
0	0.972	1.109	1.875	0.745	1.561	0.663	0.972	2.600	1.792		2.718
1	0.931	0.671	0.641	0.763	0.840	0.886	0.927	1.151	0.900	0.850	0.678
3	0.200	0.150	0.138	0.142	0.145	0.151	0.151	0.182	0.174	0.172	0.138
4	0.029	0.024	0.025	0.023	0.025	0.024	0.026	0.030	0.029	0.031	0.026
5 6	0.015	0.014	0.016	0.015	0.017	0.017	0.018	0.021	0.020	0.022	0.020
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9 10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
0	1.076	1.579	1.625	1.037	1.771	1.917	1.418	2.054	1.877	2.329	3.017
1	0.715	0.698	0.614	0.671	0.618	0.617	0.538	0.543	0.593	0.682	0.664
2	0.291	0.291	0.238	0.258	0.248	0.243	0.237	0.238	0.233	0.275	0.273
3	0.152	0.151	0.146	0.142	0.160	0.168	0.179	0.195	0.200	0.214	0.225
4	0.033	0.032	0.036	0.031	0.038	0.042	0.047	0.053	0.055	0.057	0.062
5	0.026	0.027	0.031	0.027	0.033	0.037	0.043	0.049	0.051	0.053	0.056
6	0.053	0.055	0.063	0.055	0.068	0.075	0.088	0.101	0.106	0.107	0.115
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1996	1997	1998	1999	2000	2001	2002	2003
0	2.235	3.277	3.261	3.857	3.022	2.893	4.021	2.847
1 2	0.761	0.619	0.622	0.675	0.461	0.410 0.132	0.423 0.148	0.465 0.188
3	0.248	0.243	0.251	0.263	0.270	0.264	0.247	0.248
5	0.058	0.061	0.067	0.068	0.083	0.086	0.078	0.074
6 7	0.119	0.125	0.138	0.139	0.169	0.177	0.162	0.154
8 9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 4.3: Predation mortality (M2), (Cont'd).

Species Haddock

Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
0	1.343	1.563	1.682	1.601	1.246	1.699	1.953	1.438	1.514	1.900	1.821
1	0.701	0.984	1.104	1.182	1.197	1.067	1.633	1.604	1.463	1.752	2.063
[2]	0.142	0.167	0.225	0.255	0.275	0.212	0.265	0.334	0.253	0.212	0.279
[3]	0.068	0.078	0.096	0.115	0.127	0.100	0.120	0.155	0.142	0.111	0.121
4	0.062	0.064	0.082	0.099	0.112	0.089	0.093	0.133	0.135	0.099	0.097
İ5 İ	0.050	0.052	0.054	0.058	0.059	0.053	0.062	0.071	0.072	0.059	0.063
[6	0.035	0.034	0.042	0.048	0.051	0.043	0.046	0.068	0.065	0.043	0.043
[7]	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
[8]	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
j9 j	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	·	·		<u>:</u>			·				

Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
+	+	+	+	+	+	+	+	+	+	+	
0	1.451	1.622	1.940	1.727	1.904	1.606	2.056	2.087	1.795	1.388	1.827
1	1.716	1.254	1.437	1.231	1.303	1.405	1.296	1.800	1.345	1.333	0.962
į 2 į	0.297	0.214	0.188	0.202	0.200	0.211	0.201	0.251	0.242	0.213	0.160
[3]	0.137	0.107	0.102	0.098	0.090	0.088	0.085	0.098	0.096	0.092	0.071
4	0.111	0.096	0.084	0.082	0.075	0.076	0.067	0.080	0.083	0.080	0.066
[5]	0.073	0.064	0.067	0.064	0.066	0.066	0.068	0.078	0.078	0.082	0.072
[6	0.056	0.051	0.041	0.040	0.041	0.041	0.037	0.048	0.049	0.048	0.042
[7]	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
[8 j	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
j 9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
lo i	1.739	1.722	2.139	1.811	1.847	1.885	1.588	1.746	1.831	1.521	2.164
1	1.140	0.963	0.969	1.250	0.982	1.056	0.914	0.818	0.898	1.026	0.926
2	0.158	0.158	0.127	0.148	0.139	0.133	0.126	0.121	0.118	0.142	0.137
3	0.069	0.062	0.053	0.053	0.054	0.057	0.055	0.057	0.055	0.060	0.063
4	0.057	0.055	0.044	0.045	0.043	0.049	0.046	0.046	0.047	0.048	0.049
5	0.086	0.085	0.093	0.083	0.098	0.109	0.123	0.139	0.145	0.149	0.160
6	0.040	0.041	0.038	0.036	0.039	0.045	0.047	0.050	0.053	0.052	0.056
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1996	1997	1998	1999	2000	2001	2002	2003
0	1.592	2.008	2.249	1.690	1.582	1.914	2.542	2.100
1	1.249	1.038	1.463	1.414	0.910	1.150	1.243	1.837
2	0.167	0.147	0.137	0.152	0.090	0.066	0.079	0.114
3	0.069	0.066	0.064	0.061	0.048	0.038	0.037	0.046
4	0.056	0.054	0.053	0.049	0.037	0.030	0.027	0.033
5	0.168	0.173	0.189	0.192	0.219	0.224	0.201	0.200
6	0.061	0.061	0.065	0.064	0.068	0.067	0.059	0.060
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 4.3: Predation mortality (M2), (Cont'd)

Species Herring

Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
0	1.067 0.863 0.272	0.909 0.855 0.352	0.956 0.947 0.372	0.785 0.926 0.419	0.816	0.794	0.870	0.417 0.623 0.493	0.573	0.601	
3 4 5	0.175 0.074 0.093	0.211 0.087 0.103	0.276 0.103 0.112	0.347 0.126 0.127	0.373 0.129 0.114	0.307 0.116 0.127	0.407 0.134 0.139	0.437 0.149 0.133	0.353 0.147 0.141	0.158	0.492 0.167 0.153
6 7 8	0.083	0.159 0.000 0.000	0.175 0.000 0.000	0.173 0.000 0.000	0.000	0.000	0.000	0.247	0.130 0.000 0.000	0.000	0.231 0.000 0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
0	0.582	0.728	0.566	0.480	0.466	0.422	0.590	0.427	0.457	0.380	0.416
1	0.475	0.511	0.483		0.586		0.758	0.709	0.575		
3	0.413	0.277	0.273	0.312	0.299	0.328	0.287	0.357	0.351	0.296	0.232
4 5	0.139	0.114	0.116	0.120	0.116	0.119	0.110	0.132	0.135		0.102
6	0.244	0.144	0.149	0.147	0.140	0.120	0.154	0.176	0.150	0.139	0.095
7 8	0.000	0.000	0.000	0.000	0.000	0.000	!	0.000	0.000		0.000
9	0.000	0.000			0.000	!	!	0.000			

Age	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
0	0.372	0.431	0.811	0.889	0.915	2.658	2.362	2.254	2.459	2.169	2.067
1	0.398	0.448	0.491	0.493	0.543	0.506	0.405	0.392	0.383	0.375	0.375
2	0.363	0.366	0.376	0.425	0.341	0.383	0.298	0.273	0.305	0.335	0.301
3	0.242	0.259	0.222	0.259	0.195	0.180	0.194	0.180	0.192	0.262	0.215
4	0.107	0.107	0.105	0.107	0.090	0.084	0.085	0.082	0.090	0.103	0.098
5	0.133	0.129	0.132	0.131	0.124	0.118	0.114	0.115	0.122	0.123	0.129
6	0.134	0.098	0.100	0.100	0.117	0.097	0.080	0.085	0.077	0.093	0.102
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1996	1997	1998	1999	2000	2001	2002	2003	
+	+	+	+	+	+	+	+		
0	0.671	1.169	0.713	0.713	0.538	0.471	0.671	0.576	
1	0.389	0.337	0.369	0.322	0.291	0.332	0.414	0.440	
2	0.384	0.302	0.345	0.349	0.253	0.275	0.317	0.392	
3	0.295	0.251	0.258	0.280	0.156	0.149	0.185	0.257	
4	0.118	0.107	0.116	0.112	0.082	0.081	0.099	0.115	
5 j	0.129	0.127	0.133	0.121	0.111	0.110	0.132	0.125	
6	0.121	0.124	0.121	0.108	0.057	0.069	0.082	0.146	
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	

Table 4.3: Predation mortality (M2), (Cont'd)

Species Norway pout

! - '	63 1964									
0 1. 1 0. 2 0.	021 1.015 990 1.368 609 0.906 508 0.706	0.976 1.552 1.036	0.909 1.577 1.165	0.981 1.349 1.099	1.084 1.502 1.082	1.019 2.281 1.487	0.796 2.373 1.696	0.858 2.182 1.681	1.067 1.960 1.665	1.049 2.050 1.822

	 e 1974 -++										:
0 1	0.830	0.977 1.605	0.897 2.071	0.824 1.580	0.826 1.487	0.774 1.181	1.035 1.195	0.798 1.908	0.794 1.619	0.678 1.265	0.886 1.457
	1.299 1.315										

	1985 										1995
0	0.890	0.950	1.158	0.976	0.993	0.937	0.802	0.883	0.989	0.718	1.081
2	1.398	1.536	1.447	1.350	1.049	1.109	1.103	0.958	1.132	1.267	

! -	1996								
0 1 2	0.675 2.009 1.595 1.615	0.999 1.682 1.296	1.041 1.901 1.524	0.834 1.769 1.522	0.835 1.515 1.179	0.953 1.979 1.399	1.286 2.546 1.798	0.890 2.950 2.358	

Table 4.3: Predation mortality (M2), (Cont'd)

Species Sandeel

											1973
0 1 2 3	0.911 2.081 0.671 0.867	0.885 2.053 0.685 0.887	0.877 1.934 0.714 0.892	0.831 1.558 0.599 0.800	0.889 1.377 0.515 0.700	1.138 1.548 0.531 0.673	1.117 1.652 0.575 0.688	0.709 1.334 0.541 0.628	0.697 1.065 0.414 0.564	0.925 1.555 0.477 0.573	1.434 1.488 0.489 0.586 0.420

! - '	1974										
0 1	0.958 1.213 0.383 0.507 0.325	1.300 1.155 0.408 0.551	0.859 1.152 0.403 0.545	0.593 0.895 0.395 0.522	0.722 0.918 0.403 0.540	0.720 0.861 0.390 0.510	0.922 1.052 0.497 0.651	0.866 1.282 0.542 0.668	0.979 0.808 0.414 0.587	0.790 0.865 0.382 0.550	1.183 0.752 0.394 0.588

Age 198	,									:
0 0.8 1 0.8 2 0.3 3 0.5 4 0.2	58 1.049 53 0.759 74 0.394 38 0.552	1.367 0.868 0.402 0.591	1.063 0.921 0.411 0.564	1.277 0.852 0.451 0.651	1.164 0.876 0.452 0.643	1.038 0.685 0.365 0.548	1.291 0.694 0.378 0.583	1.090 0.801 0.377 0.550	1.051 0.760 0.369 0.519	1.321 0.737 0.380 0.568

Age 1996 1997 1998 1999 2000 2001		
0 0.880 1.284 1.263 1.223 1.161 1.100 1 0.856 0.624 0.811 0.867 0.834 1.029 2 0.379 0.327 0.356 0.395 0.368 0.404 3 0.510 0.490 0.528 0.525 0.552 0.549 4 0.264 0.253 0.246 0.249 0.270 0.275	1.565 1.017 0.448 0.633	1.029 1.196 0.468 0.598

Table 4.3: Predation mortality (M2), (Cont'd)

Species Sprat

	1963										:
0 1 2 3	0.622 1.148 0.851 0.419 0.619	0.583 0.917 0.877 0.486	0.568 0.992 0.879 0.422	0.576 0.888 0.848 0.424	0.544 0.888 0.790 0.341	0.700 1.254 0.885 0.365	0.670 0.891 0.832 0.465	0.510 0.697 0.617 0.253	0.542 0.565 0.584 0.244	0.492 0.811 0.765 0.311	0.517 0.895 0.743 0.342

											1984
0		0.494	0.592	0.586	0.597	0.605	0.782	0.664	0.823	0.632	0.848
	0.582										
											0.268

										1994	1995
0 1 2 3	0.691 0.651 0.637 0.333	0.899 0.763 0.669 0.281	1.961 0.812 0.780 0.360	1.471 0.891 0.873 0.464	1.611 0.995 0.881 0.385	0.947 0.927 0.861 0.515	0.883 0.667 0.616 0.333	1.133 0.592 0.596 0.288	0.827 0.648 0.603 0.298	0.880 0.554 0.533 0.278	1.071 0.564 0.567 0.243 0.471

! - '					2000			
0 1 2 3	0.640 0.599 0.558 0.326	0.900 0.424 0.488 0.211	0.823 0.522 0.661 0.291	0.803 0.617 0.574 0.278	0.781 0.553 0.512 0.218 0.390	0.688 0.622 0.581 0.277	0.887 0.671 0.667 0.312	0.641 0.628 0.648 0.419

Table 4.3: Predation mortality (M2), (Cont'd)

Species Whiting

Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
0	1.352	1.097		0.918			!				
2	0.239	0.334		0.493			!			0.467	!
4 5	0.151	0.206	0.239	!			!				!
6 7	0.147	0.196	0.214	0.247	0.242		!				
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

! -									'		1984
 0 1 2 3 4	0.892 0.764 0.434 0.306 0.308	1.198 0.680 0.330 0.231	1.804 0.921 0.343 0.229	0.984 0.781 0.374 0.240	1.496 1.049 0.370 0.224	0.974 0.984 0.431 0.251	1.495 1.008 0.386 0.234	2.184 1.809 0.506 0.282	1.658 1.105 0.465 0.291	0.835 0.964 0.386 0.246	2.232 1.010 0.316 0.200
5 6	0.260		0.221	!		!	!				!
7 8	!!!		0.000	!		!	!				!

Age	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
0	1.079	1.525			1.914		!			1.943	
2	0.332	0.314	!	0.328		0.243	!				!
3	0.206	0.207	0.167	0.198	0.183	0.172	0.187	0.182	0.186	0.230	0.215
4	0.222	0.224	0.195	0.211	0.211	0.196	0.220	0.226	0.230	0.279	0.270
5	0.252	0.249	0.252	0.245	0.261	0.274	0.313	0.340	0.352	0.391	0.401
6	0.220	0.222	0.207	0.216	0.206	0.207	0.233	0.245	0.257	0.301	0.293
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Age	1996	1997	1998	1999	2000	2001	2002	2003
+	+	+	+	+	+	+	+	·!
0	2.000	2.529	2.370	2.890	2.438	2.497	3.501	2.572
1	1.295	1.020	1.373	1.584	0.962	1.065	1.032	1.301
2	0.370	0.291	0.303	0.339	0.167	0.153	0.179	0.205
3	0.259	0.234	0.228	0.265	0.188	0.170	0.177	0.191
4	0.309	0.291	0.287	0.330	0.280	0.265	0.264	0.276
5	0.439	0.433	0.460	0.498	0.509	0.512	0.474	0.473
6	0.333	0.313	0.330	0.362	0.325	0.330	0.314	0.322
7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table 4.4: Partial predation mortality (M2) summary for the years 1963–2003.

Prey Cod

		 				Preda	itor				 		
		Sea birds	Cod	Grey Gurnards	 Haddock	NS. Mackerel	Saithe	Raja radiata	Grey Seals	 Whiting	West Mackerel	All	
		%	%	+ %	+ %	+	%	%	+ %	+ %	++	%	Average M2
Quar-	- Age												
ter	1	22.9	46.5	1.8	 				l 3.8	l 25.0		100.0	0.260
-	2	44.9	96.5	i	–	-	_	_	3.5	i	i -i	100.0	
	3	-	33.6	i	_	-	_	_	66.4	_	i i	100.0	0.135
1	<i>Δ</i>	-		i –	_	-	_	_	100.0	_	-	100.0	0.044
1	5	-	_	1	_	-	_	_	100.0	 	i i	100.0	0.014
1	6	-	_	I	_	-	_	_	100.0	_	1	100.0	
2	1	1.7	96.1	-	_	i i	_	_	2.2	 _	: :	100.0	0.401
4	2	i i	94.6	i	_	i i	-	_	5.4		i i	100.0	
1	3	-	74.1	i –	_	i i	_	_	25.9	_	i i	100.0	
1	4	-	49.0	i –	_	i i	-	_	51.0	_ _	-	100.0	
1	5	-		i –	_	i i	_	_	100.0	_ _	: :	100.0	0.012
1	6	-	_	İ	–	-	_	_	100.0	–	-	100.0	0.013
3	0	5.8	5.0		0.0	_ 7.1	2.0	3.3		 9.1	2.8	100.0	1.156
	1	3.0	91.4	i	0.0	i i	2.0	3.3	8.6	,	2.0	100.0	0.049
1	2	-	97.2		-	-	_	_	2.8	-	-	100.0	0.089
1	3	-	29.5		-	-	_	_	70.5	-	-	100.0	0.013
1	4	-	81.5		–	i i	_	_	18.5	-	-	100.0	0.001
i	5	-	01.5	-	_ _	i i	_	_	100.0	-	-	100.0	0.000
4	0	19.0	4.7	62.2	İ	i i		_	0.3	13.8		100.0	
-	1	1	43.8	i	_ 	i i	_	_	56.2		-	100.0	0.032
i	2	-	77.1		_ 	1 1	_	_	22.9	_ _	i i	100.0	0.049
İ	3	-	21.4		_ _	i i	_	_ _	78.6	_	-	100.0	0.041
i	4	i -i				i i	_	_	100.0		i –i	100.0	0.012
i	5	i -i	_	İ		1 1	_	_	100.0	_	i i	100.0	0.007
i	6	i -i	_	i –	_ 	i i	_	_	100.0	_	-	100.0	0.015
All	0	10.6	4.9	63.6	0.0	_ 4.5	1.3	2.1	0.4	10.8	1.8	100.0	1.816
	1	9.0	76.1			_	_		5.5	8.8		100.0	0.742
i	2		93.5			i –i	_	_	6.5	_	i -i	100.0	0.344
i	3	i -i	49.1			i i	_	_	50.9		i _i	100.0	0.183
i	4	i -i	17.9			i i	_	_	82.1		i -i	100.0	0.040
i	5	i -i		i –	i –	i -i	_	_	100.0		i -i	100.0	
i	6	i -i	_	i -		j -i	_	_	100.0		i -i	100.0	

Table 4.4: Partial predation mortality (M2) summary for the years 1963-2003 (Cont'd)

Prey Haddock

Grey Grey West Sea Horse birds |Gurnards|Haddock | Mackerel | Saithe | Seals |Whiting |Mackerel | All Cod 용 ક | % 용 용 Quar- Age lter 1 38.0 0.0 22.4 100.0 0.644 1 1.4 38.2 2 94.4 1.3 0.2 4.1 100.0 0.087 3 91.6 0.1 8.3 100.0 0.016 95.2 100.0 0.025 0.3 4.5 100.0 0.024 21.6 78.4 59.8 40.2 100.0 0.025 1 66.2 0.1 100.0 0.190 0.9 0.4 9.4 23.0 2 72.5 14.2 0.4 12.9 100.0 0.043 3 90.1 4.2 5.8 100.0 0.026 87.9 12.1 100.0 0.021 5 22.4 77.6 100.0 0.026 67.5 32.5 100.0 0.017 0.7 10.6 14.0 27.1 0.0 100.0 0.937 13 0 7.6 1.1 35.3 3.6 1 29.1 0.7 69.4 0.3 0.5 100.0 0.320 2 97.2 0.3 2.5 100.0 0.031 86.1 13.9 100.0 0.026 96.3 3.7 100.0 0.019 22.2 77.8 100.0 0.023 100.0 100.0 0.002 34.2 15.6 37.7 100.0 0 1.3 9.5 1.8 0.0 0.840 1 89.2 0.5 2.5 7.8 100.0 0.091 2 98.1 0.1 1.8 100.0 0.020 83.5 16.5 100.0 0.014 59.7 40.3 100.0 0.005 91.1 100.0 0.031 8.9 100.0 100.0 0.006 8.5 İ 21.7 All 1.0 21.7 1.4 7.4 0.0 36.4 1.9 100.0 1.776 1 0.9 43.9 0.1 0.21 38.9 0.3 15.8 100.0 1.246 2 90.1 4.1 0.8 5.0 100.0 0.182 87.9 1.3 10.7 100.0 0.082 90.8 0.1 100.0 9.1 0.069 81.9 5 18.1 100.0 0.104 53.5 46.5 100.0 0.049

| 6 | _| 53.5| _| _| _| 46.5| _| _| 100.0| 0.049

Table 4.4: Partial predation mortality (M2) summary for the years 1963–2003 (Cont'd)

Prey Herring

· 		 				Preda	ıtor						
		Sea birds	Cod	 Haddock	Horse Mackerel	NS. Mackerel	Saithe	Raja radiata	Grey Seals	 Whiting	West Mackerel	All	
		%	%	+ %	+ %	%	%	%	% %	+ %	%	%	Average M2
Quar	- Age			 	 	 			 	 			
11	1	i i	29.0	0.3	i	0.7	6.5		i	63.4	i i	100.0	0.151
-	2	0.0	41.8	1.6		;	13.0	_	0.0	43.5		100.0	0.227
l	3	0.8	65.0	i	i –	_ 	32.9	_	0.0	1.3		100.0	0.112
i	4	9.2	70.8	_ _	i	-	19.7	_	0.3		-	100.0	0.046
i	5	36.8	55.7		i	-	6.0	_	1.4		i i	100.0	0.018
i	6	j _i	100.0		i –	-				i –	i -i	100.0	0.011
2	1	-i	63.7		i –	11.3	0.4	_	-	24.7	-	100.0	0.086
i -	2	0.8	61.9		_		37.2	0.0	-	0.0		100.0	0.076
i	3	6.6	54.4	i _	i	_	38.8	0.1	-	i _	i -i	100.0	0.031
i	4	21.9	35.5		i		42.5	0.2		i –	i -i	100.0	0.010
i	5	39.5	28.7		1	_	31.7	0.1	_	i –	i -i	100.0	0.019
3	0	i _i	0.6			1.2	3.6	0.5	_	31.7	13.4	100.0	0.203
i	1	i _i	12.6		i	32.5	0.6		0.0	54.4	i _i	100.0	0.266
i	2	0.8	54.1		i		12.6	_	0.1			100.0	i 0.058i
İ	3	0.7	88.2		i		11.0		0.1	i _	i Ii	100.0	0.124
İ	4	18.5	61.3			ii	19.5		0.7	<u> </u>	i Ii	100.0	0.031
İ	5	53.4	35.3		i	i _i	8.8	_	2.5	i _		100.0	0.027
İ	6	i _i	18.9		i		81.1	_	i _	i _		100.0	0.028
4	0	i _i	2.7		61.7	17.2	8.5		i _	9.1		100.0	0.673
İ	1	i Ii	52.6	i _	i _	2.2	20.4	15.2	0.0	9.7	i _i	100.0	0.043
İ	2	2.3	43.3	i _	1	i _i	45.5	8.5	0.3	0.2	i Ii	100.0	0.025
İ	3	12.4	29.6	i _	i	i _i	51.5	6.0	0.6	<u> </u>	i Ii	100.0	0.011
İ	4	29.0	24.0		1	ji	45.7	0.7	0.7	i _	i _i	100.0	0.025
İ	5	54.5	25.8		i	i _i	18.8	_	0.9	i _	i Ii	100.0	0.063
İ	6	_i _i	100.0	i _	1	ii	_		i _	i I	i Ii	100.0	0.093
All	0	_i _i	2.2		58.7	13.5	7.3	0.1	i _	14.3	3.6	100.0	0.876
İ	1	i _i	28.3	0.1	İ _	18.0	3.8	1.2	0.0			100.0	0.546
İ	2	0.5	47.7	1.0	i _	ji	19.8	0.6	0.0	30.5	i _i	100.0	0.387
İ	3	1.9	72.7	i _	i	<u> </u>	24.6	0.3	0.1	0.5	i _i	100.0	0.278
İ	4	17.4	54.5		i	ii	27.5	0.2	0.5	i _	i _i	100.0	0.112
İ	5	49.5	32.6		i	i _i	16.8	0.0	1.2	i _	i _i	100.0	0.127
İ	6	_i _i	82.7		i _	i _i	17.3	_	İ _	i _	i _i	100.0	0.133

Table 4.4: Partial predation mortality (M2) summary for the years 1963–2003 (Cont'd)

Prey Norway pout

Cod | Gurnards | Haddock | Mackerel | Mackerel | Saithe | radiata | Whiting | Mackerel | All % | % | % | % | % | % | % | % | M2 Ouar- Age 11.0 | 10.7 | 21.5 | 2 1 | 5.3 | ter 1 2 10.5 1.0 1 | 4.7 | 2 | 9.5 | 0.2 2 1.6 4.4 4.2 100.0 0.550 0.1 81.6 0.1 3 100.0 0.579 28.5 3.2 67.5 0.8 13 0 4.3 2.9 11.7 3.0 | 13.3 | 14.3 0.2 19.9 30.3 100.0 0.370 1 24.8 0.7 0.3 52.2 2.7 13.2 1.4 100.0 0.238 4.8 2 49.7 3.6 0.9 40.2 0.2 5.4 100.0 0.173 3 44.7 2.0 14.2 39.1 100.0 0.141 6.1 0.3 1.7 3.2 0.1 11.4 2.2 19.2 55.7 100.0 0 0.557 21.6 7.2 1 14.9 32.5 3.9 11.8 8.2 100.0 0.387 2 15.0 1.0 27.2 6.3 50.1 100.0 0.154 0.4 27.4 72.6 100.0 0.020 3 9.0 All 0 3.7 1.2 11.5 2.5 17.2 0.3 41.4 13.1 100.0 0.926 12.7 1.7 56.9 1.7 13.1 2.0 100.0 1.705 1 3.6 8.2 2.9 2.0 12.5 18.3 0.1 62.7 1.4 100.0 | 1.317 _| 100.0| 1.305| 22.4 2.1 67.4 1.4 6.7

Table 4.4: Partial predation mortality (M2) summary for the years 1963–2003 (Cont'd)

Prey Sandeel

						Preda	ator				 		
		Sea	Cod	Grey Gurnards	 Haddock	Horse Mackerel	NS. Mackerel	Saithe	Raja radiata	 Whiting	 West Mackerel	All	
		%	%	+ %	+ %	+ %	+ %	%	+ %	+ %	++	%	Average M2
Quar-	Age			+ 	+ 	+ 	 		+ 	+ 	 		
1	1	1.7	4.8	1.2	18.1	 	8.2	17.3	4.7	39.1	5.0	100.0	0.272
	2	27.2	17.7		4.6	i	i _i	7.5	1.6	39.7		100.0	0.050
	3	i _i	39.0	13.8	7.0	i _	i _i	0.0	8.4	31.8	i _i	100.0	0.008
	4	i _i	58.0	3.7	16.2	İ _	j _i	_	2.9	19.1	i _i	100.0	0.011
2	1	4.7	10.0	3.2	12.2	_	31.9	19.0	0.5	16.8	1 1	100.0	0.703
	2	9.3	13.4	8.5	9.1	_	21.5	5.6	5.8	26.3	0.4	100.0	0.273
	3	30.6	15.5	6.5	5.3	_	18.2	5.7	5.5	12.6	0.2	100.0	0.310
	4	_	23.2	5.5	7.3	_	34.0	7.2	5.1	17.6	0.1	100.0	0.171
3	0	3.3	1.4	1	11.5	18.4	8.2	1.4	1.0	12.3		100.0	0.871
	1	10.5	9.8	1	1.9	0.6	3.8	0.7	2.2	33.3		100.0	0.075
	2	21.1	10.7	•	4.0	_	5.1	0.1	0.5	38.9		100.0	0.094
	3	45.6	3.2	•	3.8	_	11.8	_	0.3	1		100.0	0.205
	4	_	1.5		19.1	_	48.2	_	_	13.9		100.0	
4	0	5.3	3.8	I	28.6	0.8	4.8	0.3		28.7		100.0	0.163
	1	_	10.3	!	9.3	_	4.4	_	1.7			100.0	0.039
	2	20.2	18.8	1	_	_	_	_	1.5	57.8		100.0	0.030
	3	<u> </u>	14.3		0.2	_		_	0.8	80.6		100.0	0.082
	4	_	14.7	•	. –	_	_	_	0.4	1		100.0	
All	0	3.6	1.8	1	14.2	15.6	7.7	1.2	1.1	14.9		100.0	1.034
	1	4.2	8.7	1	12.8	0.0	23.1	16.6	1.7			100.0	1.089
	2	14.5	13.7	1	6.9	_	14.2	4.3	1	32.6		100.0	0.447
	3	31.2	11.4	1	4.2	_	13.3	2.9		1		100.0	
	4	_	15.9	3.9	8.9	_	28.2	3.1	2.4	33.8	3.8	100.0	0.394

Table 4.4: Partial predation mortality (M2) summary for the years 1963–2003 (Cont'd)

Prey Sprat

		 			Preda	ator					
		Cod	Grey Gurnards	 Haddock	Horse Mackerel	NS. Mackerel	 Saithe	 Whiting	West Mackerel	All	 Average
		 %	+ %	+ %	+ %	% %	% %	+ %	%	8 8	M2
Quar-	Age	 	 	 	+ 		 	 	; 	 	
ter	1	10.5								100.0	
1	1	10.7	_	0.8	-	_	0.0	1	-	100.0	0.306
	2	20.7	-	1.2	-	-	5.1	73.1	-	100.0	0.301
	3	22.8	-	0.0	-	_	4.7	72.5	-	100.0	0.254
	4	27.3						72.7	_	100.0	0.422
2	1 2	2.1	1.5	0.0	5.9		0.1	76.9	4.7	100.0	0.217
	3	26.3	0.7	0.1	-	14.0	_	58.9	0.1	100.0	0.081
		19.7	-	-	–	33.5	–	46.7	-	100.0	0.041
	4 0	0.4	 4.0	 0.0	l	72.6	 0.0	27.0 7.8		100.0	0.015
3	1	0.0			87.7	0.4	0.0		0.0	100.0	0.554
	2		0.4	0.4	-	23.2	-	74.6	0.7	100.0	0.148
	3	1.5	-	-	-	13.2 13.1	-	84.6 83.3	0.7	100.0 100.0	0.162 0.034
	4] 3.5	-	-	-	13.1	-	100.0	-	100.0	0.034
 4	0	0.3	 1.2	–	 24.7	 3.4	–		_ 28.0	100.0	0.001
4 	1	0.3 7.7	1.2	-	24./	12.9	 0.0	42.4 77.5	28.0 1.8	100.0	0.227
	2	1	-	-	-	3.0	0.0	I	0.3	100.0	
	3	10.6 8.4	–	-	-	25.3	0.2	85.9 65.2	0.3 1.0	100.0	0.174
	4	11.9	–	–	-	⊿ɔ.ɔ 	l 0.T	88.1	1 1.0	100.0	0.015
 All	0	0.1	 3.2	0.0	 69.4	_ 1.3	 0.0	88.1 17.9	_ 8.2	100.0	0.180
I WII	1	6.0	0.5	0.0	1	8.5	0.0	81.1	8.2 1.7	100.0	0.761
	2	14.6	0.5	0.4	1	5.3	2.2	77.2	0.2	100.0	0.766
	3	19.9] U.I	0.5	-	5.3 6.4	3.5	77.2	0.2 0.0	100.0	0.717
	4	22.1	–	l 0.0	-	!		76.1		100.0	!!
I	4	22.1	_	_	_	1.8	-	/0.1	ı _	100.0	0.617

Table 4.4: Partial predation mortality (M2) summary for the years 1963–2003 (Cont'd)

Prey Whiting

		Predator												
		Sea birds	Cod	Grey Gurnards	 Haddock	Horse Mackerel	NS. Mackerel	 Saithe	Raja radiata	Grey Seals	 Whiting	West Mackerel	All	
		8	%	%	%	%	%	8	%	+ %	%	%	%	Average M2
	r- Age			ļ	ļ	ļ			!	 	ļ	ļ		
ter					!	!								
1	1	1.3	40.3	21.6	_	_	_	0.1		0.1			100.0	0.506
	2	_	95.8	_	_	! _	_	0.3		1.6			100.0	0.142
	3	_	89.8	_	_	! _	_	0.2		9.9		_	100.0	0.095
	4	_	67.1	_	_	_	_	0.0	_	32.9	-	_	100.0	0.096
	5	_	49.7		_	_	_	_	_	50.3		_	100.0	0.087
	6	_	73.5		_	_	_	_	_	26.5		_	100.0	0.059
2	1	0.4	36.5		_	_	_	0.3	1	0.2		_	100.0	0.284
	2	_	93.1		_	_	_	6.4		0.4		_	100.0	0.112
	3	_	88.3		_	_	_	9.8	_	1.8		_	100.0	0.068
	4	_	82.4		_	_	_	14.2	_	3.4		_	100.0	0.085
	5	_	68.9	_	_	_	_	19.6	_	11.5	_	_	100.0	0.054
İ	6		72.5	_	_	_	_	23.3		4.2	_	_	100.0	0.068
3	0	0.5	4.7		0.0	16.7	0.1	4.3		0.0	49.4	0.9	100.0	0.744
İ	1	i _i	62.9	25.4	İ _	İ _	_	9.7	l _	0.5	1.4	j _j	100.0	0.087
İ	2	_i _i	97.8	i _	j _	i _	i _i	0.0	i _	2.2	i _	i _i	100.0	0.029
İ	3	i _i	77.8	i _	j _	i _	i _i	1.5	i _	20.8	i _	i _i	100.0	0.017
İ	4	i _i	64.9	i _		1	i _i	4.2	İ _	30.9	İ _	i _i	100.0	0.015
i	5	i -i	49.1		:	i I	ii	1.5		49.4	i –	i [–] i	100.0	0.016
i	6	i -i	35.1		į.	i –	i _	6.8		58.1		i [–] i	100.0	0.005
14	0	1.0	2.6		0.6	i -	i	2.2		0.2		i [–] i	100.0	0.906
i	1	i i	74.6			i -		0.1	10.9	14.0	İ	i [–] i	100.0	0.136
i	2	i -i	79.2	1	i –	i -	i _	0.0		15.7	-	i -i	100.0	0.064
i	3	i -i	45.1		i _	i -	i _			54.9		i -i	100.0	0.053
i	4	i _i	34.1	_	1	1		_	i -	65.9	-	i –i	100.0	0.058
i	5	i -i	9.4		i	i I	_	_	_	90.6		i -i	100.0	0.136
i	6	-	33.7	-	İ	i	i		i	66.3		i -i	100.0	0.122
All	0	0.8	3.6	49.9	0.3	7.5	0.1	3.1	0.1	0.1		0.4	100.0	1.650
	1	0.8	45.8		i	i	i	1.0		2.0			100.0	1.013
i	2	i i	92.0		i –	_	-	2.2		3.9			100.0	0.348
i	3	-	78.3	i –	i	i	_	3.1	i	18.6			100.0	0.233
i	4	-	64.5		1	1	_	5.0		30.5		-	100.0	0.254
i	5	-	34.4		-	-	_	3.7		61.9		-	100.0	0.293
1	6	-	53.4		-	-	_	6.4		40.2		-	100.0	0.253
		_		· –	· –	· –			· –		· –	 		

Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003.

Prey Cod

 		Predator											
 		Sea birds	Cod	Grey Gurnards	 Haddock	NS. Mackerel	Saithe	Raja radiata	Grey Seals	 Whiting	West Mackerel	All	
 		%	%	+ %	+ %	+	%	+	} %	+	++	 	Average M2
Quar ter	- Age			 	 					 	;		
11	1	27.6	39.2	3.8	 	i i			9.0	20.5		100.0	 0.056
i -	2		89.2	1	i -	i -i	_	_	10.8		i -i	100.0	
i	3	-	11.7		_ _	i i	_	_ _	88.3	. –	i i	100.0	
i	4	i -i		i –	i _	i i	_		100.0		i i	100.0	
i	5	i ⁻ i	_		i _	i i	_	i _	100.0		i [–] i	100.0	i 0.007i
i	6	i _i	_		i _	i i	_	i _	100.0	i _	i _i	100.0	0.007
2	1	2.5	90.4		i _	i i		i _	7.1		i i	100.0	0.065
İ	2	i _i	83.4		i _	i i	_	i _ i	16.6		i i	100.0	0.012
i	3	i Ii	44.5		i _	i i	_	i _	55.5		i Ii	100.0	0.020
ĺ	4	_i _i	19.0		İ _	1 1	_	i _ i	81.0	İ _	i _i	100.0	0.004
İ	5	i _i	_	İ _	İ _	i i	_	i _	100.0	İ _	i i	100.0	0.006
	6	_	_	_	l _	_	_	_	100.0		_	100.0	0.019
3	0	3.4	2.1	1	0.0	0.6	1.8	2.4	0.5		2.4	100.0	
	1	_	73.9	_	_	_	_	_	26.1	. –	_	100.0	
	2	_	89.2		_	_	_	_	10.8		_	100.0	
	3	_	7.3		_	_	_	_	92.7		_	100.0	
	4	_	40.2	_	_	_	_	_	59.8	. –	_	100.0	
	5	_	_		_	_	_	_	100.0		_	100.0	
4	0	11.5	1.9	1	_	_	_	_	0.3			100.0	
!	1	_	20.9	_	ļ _	_	_	_	79.1		_	100.0	0.012
!	2	_	49.6		<u> </u>	_	_	_	50.4		_[100.0	
ļ	3	_	7.3	! _	! _	_	_	_	92.7	: -	i i	100.0	
ļ	4	_	_	_	<u> </u>	_	_	_	100.0		_	100.0	
ļ	5	_	_	! –	! _	_	_	_	100.0	! –	! <u>-</u> !	100.0	
	6	-				_		_	100.0	! _ =	_	100.0	
All	0	6.4	2.0		0.0	0.4	1.1	1.5	0.4			100.0	
!	1	12.2	63.3	1	_	-	_	_	14.9	1	-	100.0	
	2	-	80.2		-	i i	_	_	19.8	i –	i i	100.0	
	3 4	-	21.1		<u> </u>	-	_	_	78.9	. –	-	100.0	
	-	-	4.8	-	-	-	_	_	95.2		-	100.0	
	5 6	-	_	-	-	-	_	-	100.0		-	100.0	
I	О		_	_	_	_	_	_	100.0	_		100.0	0.034

Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003 (Cont'd).

Prey Haddock

Grey Grey West Sea Horse birds |Gurnards|Haddock | Mackerel | Saithe | Seals |Whiting |Mackerel | All Cod 용 용 | % % 용 Quar- Age lter 1 28.3 49.6 0.0 20.6 100.0 0.160 1 1.5 2 90.0 2.6 0.5 6.9 100.0 0.015 3 77.1 0.1 22.8 100.0 0.003 14.8 100.0 0.004 84.8 0.4 100.0 0.010 6.4 93.6 26.9 73.1 100.0 0.007 1 54.4 0.3 100.0 0.037 2 1.2 1.2 14.0 28.9 2 20.1 16.2 100.0 0.008 62.7 1.1 3 73.4 6.9 19.7 100.0 0.004 62.8 37.2 100.0 0.003 5 6.4 93.6 100.0 0.011 67.8 100.0 0.004 32.2 7.0 11.8 32.4 0.0 100.0 0.254 13 0 0.6 15.1 0.9 28.1 4.2 1 17.9 0.8 80.3 0.5 0.5 100.0 0.086 100.0 0.004 2 90.4 0.5 9.1 54.2 45.8 100.0 0.004 79.9 20.1 100.0 0.002 95.8 100.0 0.009 4.2 100.0 0.001 100.0 22.7 19.9 18.8 100.0 0 1.3 1.5 0.0 35.8 0.218 1 80.5 0.6 7.5 11.4 100.0 0.016 0.003 2 93.1 0.2 6.7 100.0 53.9 100.0 0.003 46.1 31.5 68.5 100.0 0.001 97.2 100.0 0.015 2.8 100.0 100.0 0.003 All 0.91 14.3 17.3 1.2 6.3 26.1 0.0 31.6 2.2 100.0 0.472 0.1 100.0 1 0.9 31.3 0.21 51.5 0.6 15.3 0.299 2 83.4 6.6 2.4 7.7 100.0 0.030 64.8 2.0 33.2 100.0 0.013 69.2 30.6 100.0 0.2 0.011 5 4.8 95.2 100.0 0.046 21.7 78.3 100.0 0.015

Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003.

Prey Herring

		Predator										 	
		Sea birds	Cod	 Haddock	Horse Mackerel	NS. Mackerel	Saithe	Raja radiata	Grey Seals	 Whiting	West Mackerel	All	
		%	%	+ %	+ %	+	8	+ %	* %	+ %	++	%	Average M2
Quar-	Age				ļ								
ter	_	!!!											
1	1	!	23.3	I		0.4	9.2	_	! -	66.7		100.0	
!	2	0.1	34.3		_	ļ —	20.6		0.0	43.3		100.0	0.045
!	3	0.9	52.1		_	ļ —	45.1	_	0.1	1.8	-	100.0	0.025
!	4	11.2	59.5		! –	_	28.5	_	0.8	_	-	100.0	0.010
!	5	43.5	44.5		_	_	8.6	_	3.4	_	-	100.0	0.004
	6	-	100.0		! –			_	_		-	100.0	0.002
2	1	-	61.1		! –	3.3	0.8		_	34.8	: -:	100.0	
ļ	2	1.0	49.4		! –	! _	49.5	0.1	_	0.1	_	100.0	0.016
!	3	7.3	40.0		_	ļ —	52.6	0.2	_	_	-	100.0	0.007
ļ	4	23.0	24.1		! –	! _	52.7		_	! –	_	100.0	0.002
	5	41.0	18.7		! -	_	40.2	0.1	_	! -	_	100.0	0.005
3	0	-	0.5		44.8	0.1	5.2	0.6		24.3		100.0	0.050
!	1	-	14.7		! –	4.9	1.4	_	0.0			100.0	0.035
ļ	2	0.9	39.8		! _	! _	18.4	_	0.3		_	100.0	
ļ	3	1.0	77.5		! _	! _	21.2	_	0.2	! _	_	100.0	0.021
ļ	4	22.7	42.5		! _	! _	33.1	_	1.8	! _	_	100.0	0.006
	5	59.3	22.3		_	_	12.6	_	5.8	l _	_	100.0	0.006
	6	_	7.4		! _	_	92.6	_	_	_	_	100.0	
4	0	_	1.7	I	77.4	3.1	8.8	_	_	7.6		100.0	0.188
	1	_	31.6		! _	0.5	32.1		0.0	11.4		100.0	0.008
ļ	2	2.4	25.5		_	_	60.8	10.5	0.5	0.3	<u> </u>	100.0	0.006
ļ	3	11.4	19.5		_	_	61.4	6.6	1.0	<u> </u>	<u> </u>	100.0	0.003
ļ	4	26.7	16.6		! _	! _	54.7	0.8	1.2	! _	ļ _	100.0	0.007
	5	54.5	19.3		_	_	24.4	_	1.8	_	_	100.0	
	6	_	100.0		_	_	_	_	_	_	_	100.0	0.015
All	0	_	1.4			2.5	8.1		_	11.1		100.0	0.238
	1	_	25.6		_	2.6	7.1		0.0	62.2		100.0	0.089
	2	0.6	37.5		_	_	29.2	0.8	0.1			100.0	0.079
	3	2.3	58.2	. –	_	_	38.1		0.2	1	_	100.0	0.056
	4	19.4	40.2		_	_	39.1		1.1	_	_	100.0	
	5	51.9	23.2	_	_	_	22.4		2.5	_	_ [100.0	
	6	_	69.1	_	_	_	30.9	_	_	_	_	100.0	0.025

Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003 (Cont'd)

Prey Norway pout

Grey Horse NS. Raja West Cod | Gurnards | Haddock | Mackerel | Mackerel | Saithe | radiata | Whiting | Mackerel | All % | % | % | % | % | % | % | % | M2 Ouar- Age ter 7.0 21.2 21.4 2.1 100.0 0.110 1 2 12.9 4.5 6.3 1.9 100.0 0.121 7.0 2.1 82.8 3.5 100.0 0.160 2.9 0.0 89.1 2 1 3.2 0.3 0.1 100.0 0.197 5.4 3.5 2 8.1 0.1 82.7 0.1 100.0 0.163 3 17.9 6.5 74.7 100.0 0.164 0.9 2.7 1.9 13 0 2.9 5.9 11.9 18.0 0.2 18.5 38.0 100.0 0.096 1 15.1 8.7 0.6 0.0 59.7 2.6 11.8 1.4 100.0 0.071 2 33.9 7.4 1.3 51.3 0.2 6.0 100.0 0.045 3 31.9 4.9 20.8 42.3 100.0 0.031 1.7 3.5 2.2 0.3 10.1 3.3 25.9 0.4 52.7 100.0 0.131 0 14.7 37.5 1 14.8 1.8 4.7 11.9 14.7 100.0 0.098 2 10.1 0.2 31.3 7.6 50.1 100.0 0.040 0.6 15.5 84.5 100.0 0.006 3 1.8 All 0 2.5 2.6 10.8 3.0 22.6 0.3 38.3 18.0 100.0 0.227 7.5 0.4 59.3 1.9 11.4 3.2 100.0 0.476 1 8.1 8.2 2.3 1.5 11.4 11.9 6.0 0.01 66.9 100.0 | 0.369 14.2 4.3 73.8 1.5 6.2 100.0 | 0.362 |

Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003 (Cont'd)

Prey Sandeel

 ļ		 				Pred	ator				 		
		Sea birds	Cod	Grey Gurnards	 Haddock	Horse Mackerel	NS. Mackerel	Saithe	Raja radiata	 Whiting	West Mackerel	All	
		%	%	+ %	+ %	+ %	%	%	+ %	+ %	%	%	Average M2
 Quar- ter	· Age			+ 	+ 	+ 	+ 		+ 	+ 	 		+
11	1	2.0	3.7	2.9	15.6	i	 3.7	25.0	6.7	30.9	9.5	100.0	0.061
i	2	30.3	13.8		6.0	i –		10.5		33.0		100.0	0.012
İ	3	i _i	27.6	28.9	7.5	i 🗆	i _i	0.0	9.2	26.8	i _i	100.0	0.002
i	4	i Ii	47.6	8.7	19.6	i –	i _i	_	3.6	20.5	i _i	100.0	0.003
2	1	6.5	8.9	10.1	15.2	İ _	8.5	28.7	0.8	17.3	4.1	100.0	0.125
	2	11.0	9.0	22.7	10.6	_	4.4	7.9	8.2	25.2	0.9	100.0	0.057
	3	35.1	10.0	17.2	6.2	_	3.3	8.0	7.5	12.5	0.4	100.0	0.066
	4	_	19.2	18.2	10.3	_	9.0	12.6	8.6	21.6	0.3	100.0	0.029
3	0	2.8	0.8	1	8.6	15.4	0.9	1.7	1	10.0		100.0	0.240
	1	10.1	5.7	13.1	2.1	0.6	0.6	0.9	2.6	24.5	39.8	100.0	0.018
	2	23.8	7.5	1	4.2	_	0.7	0.1	0.6	33.4		100.0	0.020
	3	47.9	2.2	10.7	2.7	_	1.4	_	0.4	13.1	21.6	100.0	0.047
	4	_	1.9	14.6	20.5	. –	9.4	_		23.9	29.7	100.0	0.016
4	0	4.5	2.1	37.7	24.2	0.5	0.8	0.2	1	20.2	8.1	100.0	0.049
	1	_	6.6	18.6	7.7	_	0.6	_	2.3	63.8		100.0	0.009
	2	22.5	12.3		_	_	_	_	2.0	59.5		100.0	0.007
	3	_	9.7	9.9	0.4	_	_	_	1.1	78.9	_	100.0	0.019
	4	_	11.3	3.4	_	_	_	_	0.6	84.6		100.0	0.020
All	0	3.1	1.0	1	11.2	1	0.9	1.4	1.2	11.8		100.0	0.290
	1	5.2	7.0	1	1	0.0	6.1	24.0	2.7	23.8		100.0	0.213
	2	16.9	9.6	1	7.9	_	2.8	6.1	1	30.3		100.0	0.095
	3	34.1	7.5		4.2	_	2.1	3.9	4.1	22.3		100.0	
	4	_	14.0	12.6	9.9	_	6.0	5.5	4.1	41.0	6.9	100.0	0.068

Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003 (Cont'd)

Prey Sprat

					Preda	ator					
		 Cod	Grey Gurnards	 Haddock	Horse Mackerel	NS. Mackerel	 Saithe	 Whiting	West Mackerel	All	
		%	* %	+ %	+ %	8	* %	% %	%	%	Average M2
 Quar- ter	Age	+ 	+ 	+ 	+ 	+ 	+ 	+ 	+ 	 	+
1	1	8.0	<u> </u>	0.8	<u> </u>	_	0.0	91.2	i _i	100.0	0.055
İ	2	15.3	i _	1.5	i _	i _i	8.6	74.7	i _i	100.0	0.061
İ	3	18.3	i _	0.0		i _i	7.3	74.4	j _i	100.0	0.056
	4	20.4		_	_	_	_	79.6	_	100.0	0.090
2	1	1.5	1	0.1	7.2		0.2	1		100.0	0.044
	2	24.4	2.3	0.1	_	3.0	_	70.0	0.2	100.0	0.014
	3	24.7	l _	l _	_	9.3	_	66.1	_	100.0	0.005
	4	0.8	_	_	_	31.9	_	67.3		100.0	0.001
3	0	0.0	7.5	0.1	86.3		0.0	1	0.1	100.0	0.132
	1	0.9	1.1	0.6	_	3.3	_	92.0	2.2	100.0	0.021
	2	1.6	_	_	_	1.5	_	95.0	1.9	100.0	0.029
	3	3.9	_	_	_	1.4	_		_	100.0	0.006
	4	_	_	_	_	_	_	100.0	_	100.0	0.000
4	0	0.1	2.0	_	18.6	0.7	_	30.5	48.0	100.0	0.066
	1	6.5	_	_	_	2.5	0.0	1	4.2	100.0	0.020
	2	8.9	_	_	_	0.5	0.2	1	0.6	100.0	0.038
	3	8.6	_	_	_	5.4	0.2	1	2.9	100.0	0.003
	4	10.6	_	_	_	_	_	89.4	_	100.0	0.038
All	0	0.0	5.7	0.0	1		0.0	1	16.1	100.0	0.198
	1	4.6	1.5	0.4		1.6		1		100.0	0.140
	2	11.6	•	0.6	_	0.7		1		100.0	0.141
	3	17.2	. –	0.0	_	1.0		1		100.0	
	4	17.3	_	_	_	0.3	_	82.4	_	100.0	0.129

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Table 4.5: Partial predation mortality (M2) summary for the years 1994–2003 (Cont'd).

Prey Whiting

							Predator					 		
		Sea birds	Cod	Grey Gurnards	 Haddock	Horse Mackerel	NS. Mackerel	 Saithe	Raja radiata	Grey Seals	 Whiting	West Mackerel	All	
		8	ફ ફ	%	%	%	%	%	%	%	%	%	%	Average M2
1	- Age			ļ	ļ	ļ	ļ		ļ		ļ			
ter					!		!		ļ			!!!		
1	1	1.2	24.6	1	_	_	! –	0.1		0.2			100.0	0.145
	2	-	91.0	_	-	-	-	0.5		4.3	1		100.0	0.026
	3	-	74.6	_	1	-	-	0.3		24.9	1	-	100.0	0.019
	4	-	41.0	i –	i	-	-	0.0	-	59.0		-	100.0	0.028
	5 6	-	25.0	-	-	-	-	–	-	75.0		-	100.0	0.030
	6 1		48.5	_ 55.7	-	-	-	_		51.5		-	100.0	0.016
2	2	0.3	20.0		-	-	-	0.2		0.4		-	100.0	0.089
	∠ 3	-	89.3		-	1	-	9.3		1.3		· -	100.0	0.019
	3 1	-	79.2 70.7	i –	-	-	-	15.1 19.7		5.7 9.6		-	100.0 100.0	0.011
	4	-	48.9	-	-	-	-	23.1		9.6 28.0		-	100.0	0.015
-	5 6	-		-	-	-	-	23.1	i –	28.0 11.2	. –	-	100.0	0.011
 3	0	-	59.0 3.0	44.6	0.0	14.2	0.0	29.8 5.1		0.0	. –	_ 1.0	100.0	0.013
3	1	0.5		1	1	14.2	0.0	1	1	1	1	1 1		
	2	-	38.4	48.3	-	-	-	10.8		0.9		-	100.0	0.025
	2	-	93.4	: -	-	-	-	0.1		6.6		· -	100.0	0.005
	3	-	51.4	-	i	-	-	1.5	-	47.1		·! -!	100.0	0.004
	4 5	-	37.0		-	-	-	3.5	-	59.5	. –	-	100.0	0.004
	5 6	-	21.3	_	-	-	-	1.0		77.6	. –	-	100.0	0.005
	0	-	16.1		0.4	-	-	4.1		79.9		· -	100.0	0.002
4	1	0.6	1.0 53.3			-	-	1.5 0.1		0.2		-	100.0 100.0	0.420
-	2	-		0.6	-	-	-	0.1		31.3		-		0.031
!	2	-	54.8	-	-	-	-	0.0	1.3		_	-	100.0	
-	3 1	-	17.9	! —	-	I	-	–	-	82.1 86.0		-	100.0	0.018
	4	-	14.0		-	-	-	–	-	86.0 96.7		-	100.0 100.0	0.023
-	5	-	3.3		-	-	-	–	-	96.7 85.9	. –	-	100.0	0.066
 All	0		14.1 1.6		0.3	4.6	0.0	_ 2.7	0.1	85.9 0.1		_ 0.3	100.0	0.048 0.619
 ATT	1	0.5	27.4	1	i	1	0.0	1.0		0.1 3.7			100.0	0.619
	2	0./	82.9	i	i –	-	-	3.0	1	10.8	1		100.0	0.289 0.064
-	3	-	82.9 54.2	-	i	-	-	3.0 3.4		10.8	1		100.0	0.064
-	3 1	-	38.4		i	-	-	3.4 4.5		42.3 57.0		-	100.0	0.053
	4	-	38.4 14.6	_	-	i	-	4.5 2.4		83.0	. –	-	100.0	0.070
-	5 6	-			-	1	-	2.4 5.1				-	100.0	
1	О	_	28.5	_	_	_	_	1 2.1	_	66.4	_	·I —I	100.0	0.079

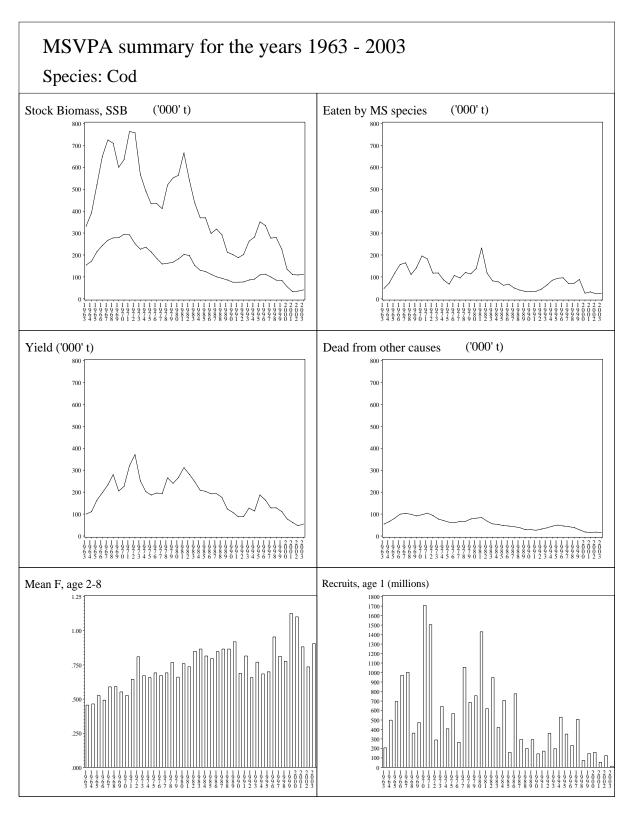


Figure 4.1: MSVPA summary.

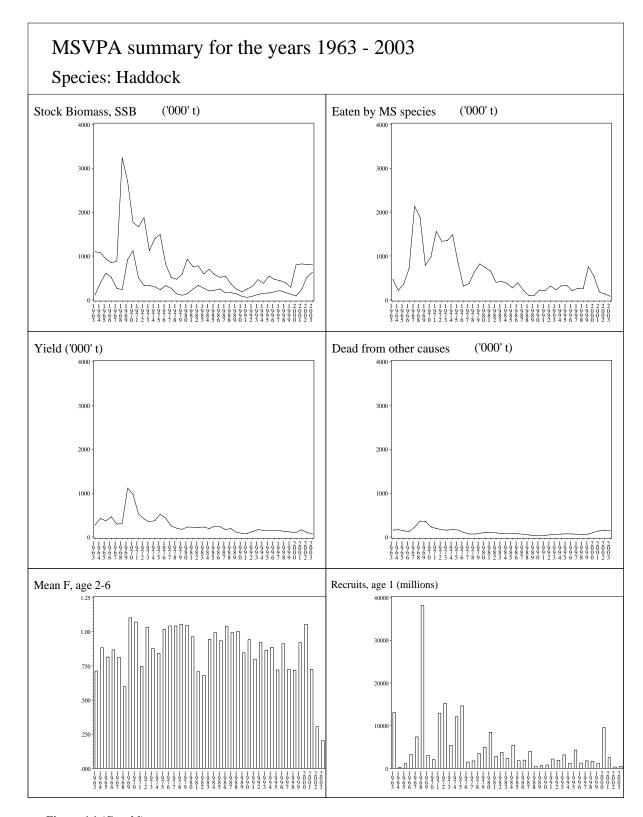


Figure 4.1 (Cont'd)

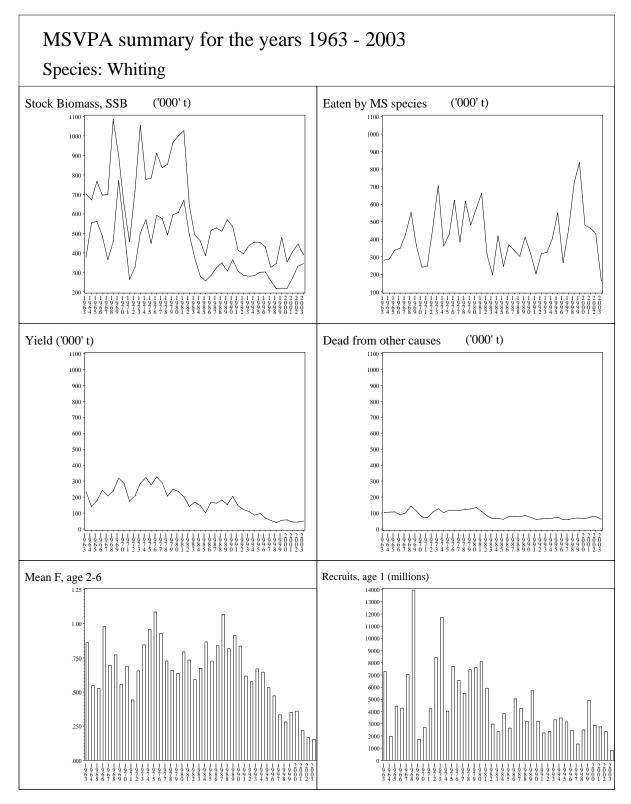


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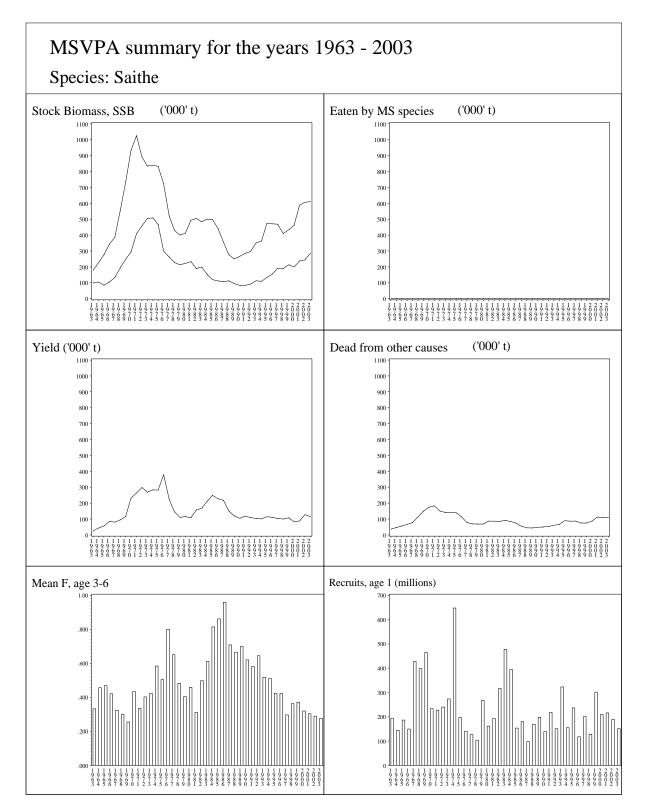


Figure 4.1 (Cont'd)

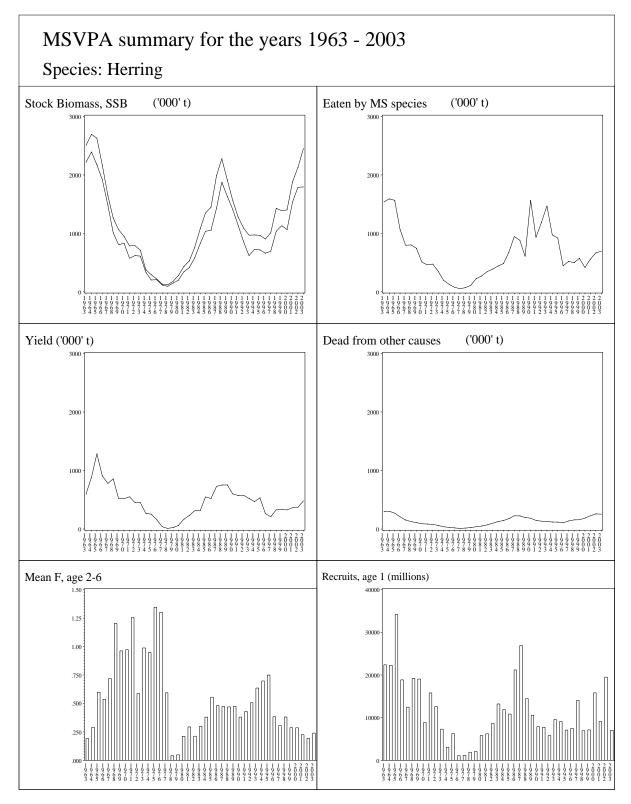


Figure 4.1 (Cont'd)

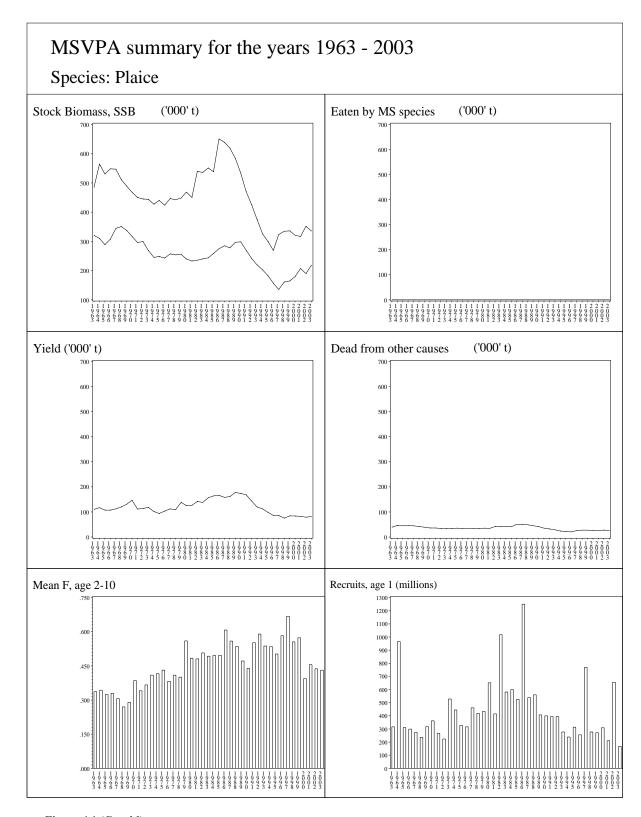


Figure 4.1 (Cont'd)

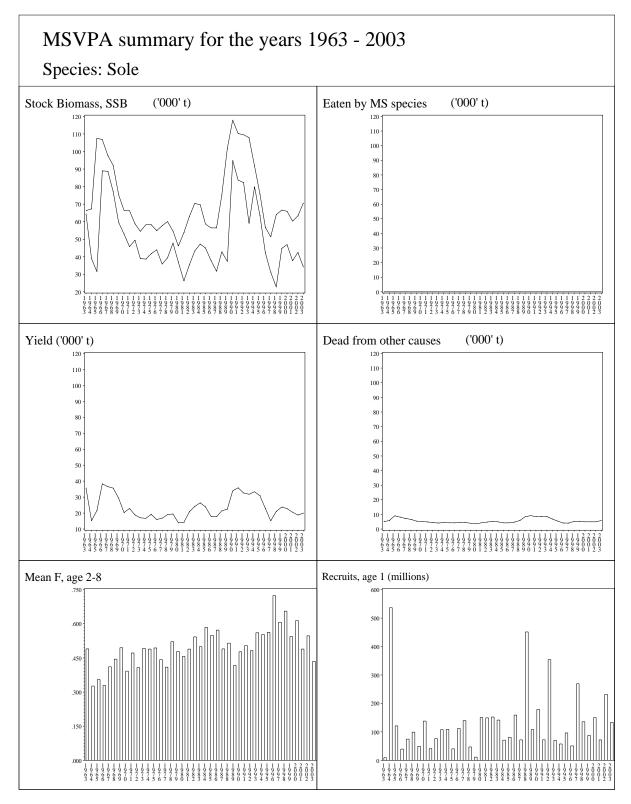


Figure 4.1 (Cont'd)

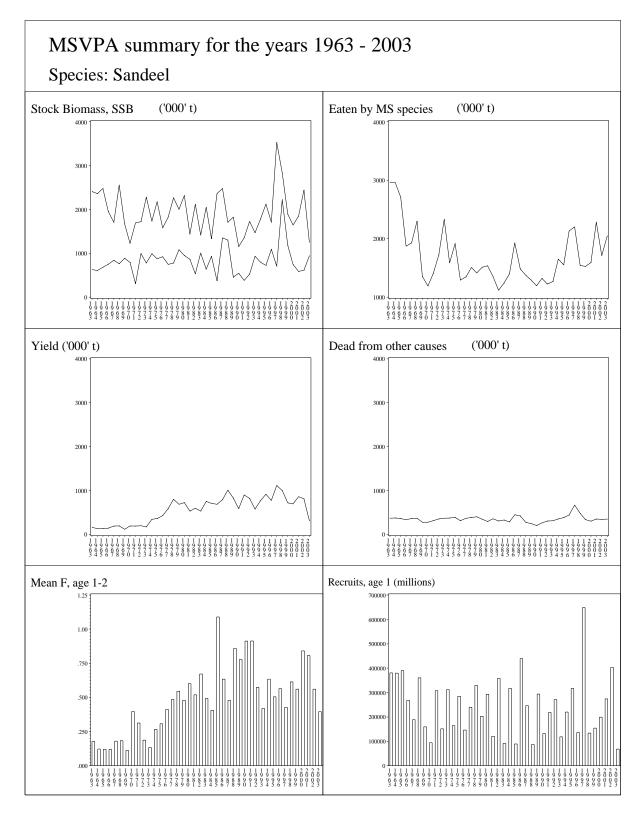


Figure 4.1 (Cont'd)

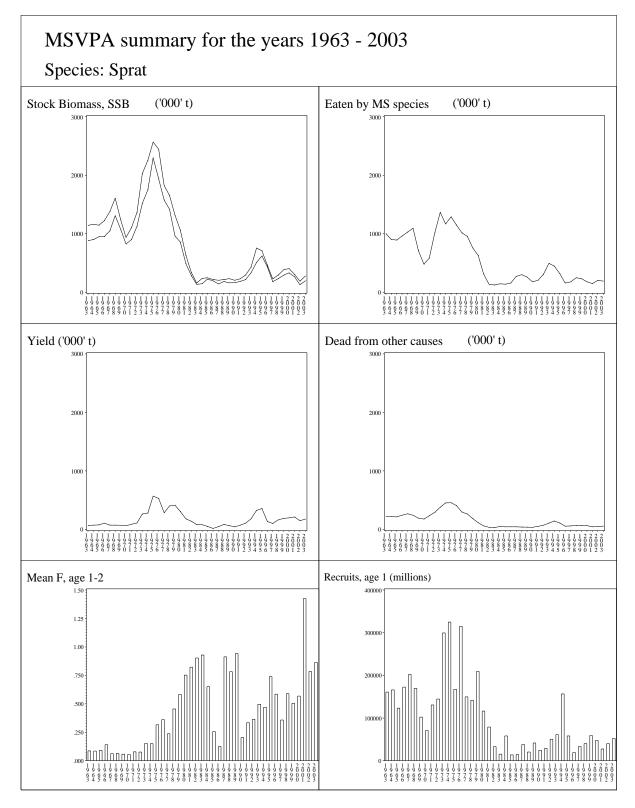


Figure 4.1 (Cont'd)

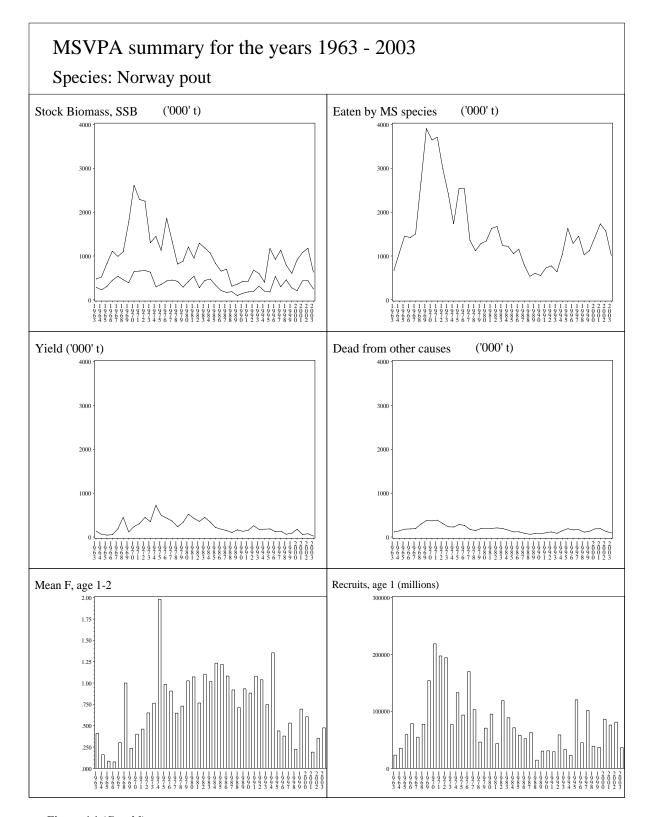


Figure 4.1 (Cont'd)

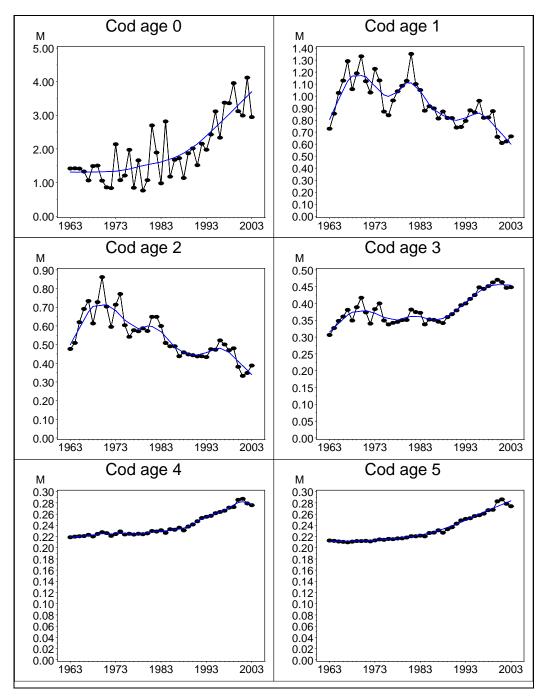


Figure 4.2: Natural mortalities (M1+M2) from MSVPA key-run, estimated values and Loess fitted trend line.

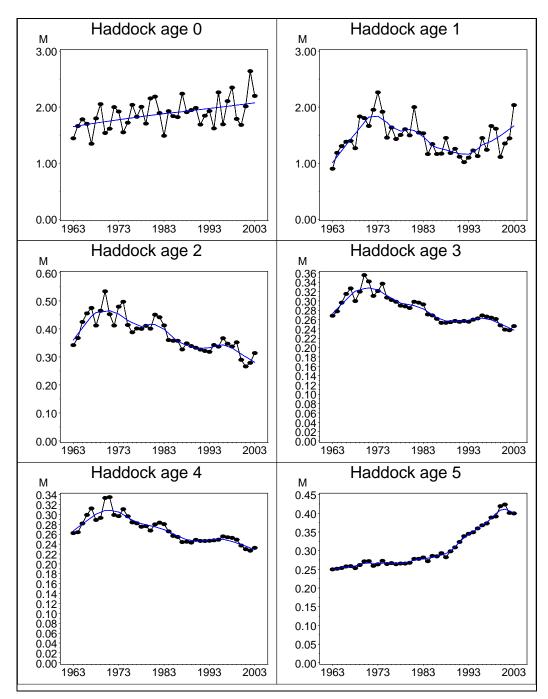


Figure 4.2: Natural mortalities (M1+M2) from MSVPA key-run, estimated values and Loess fitted trend line (cont'd).

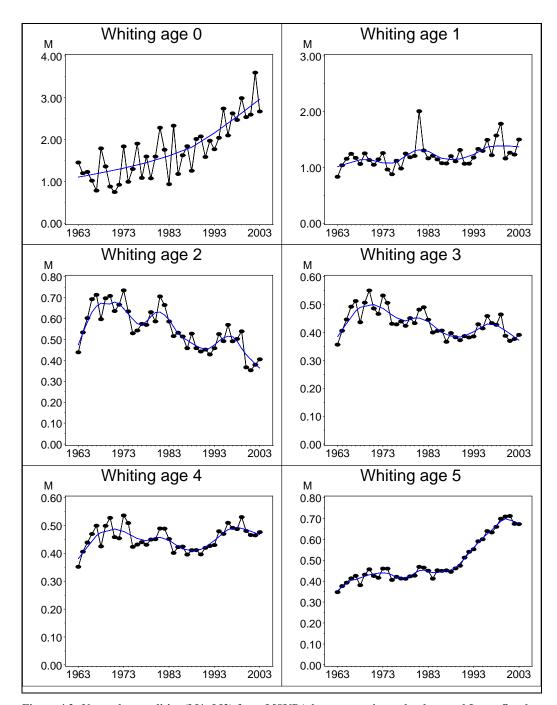


Figure 4.2: Natural mortalities (M1+M2) from MSVPA key-run, estimated values and Loess fitted trend line (cont'd).

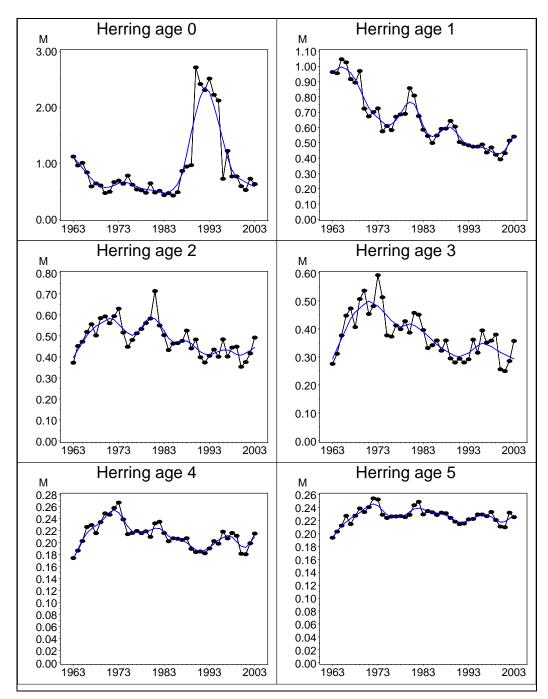
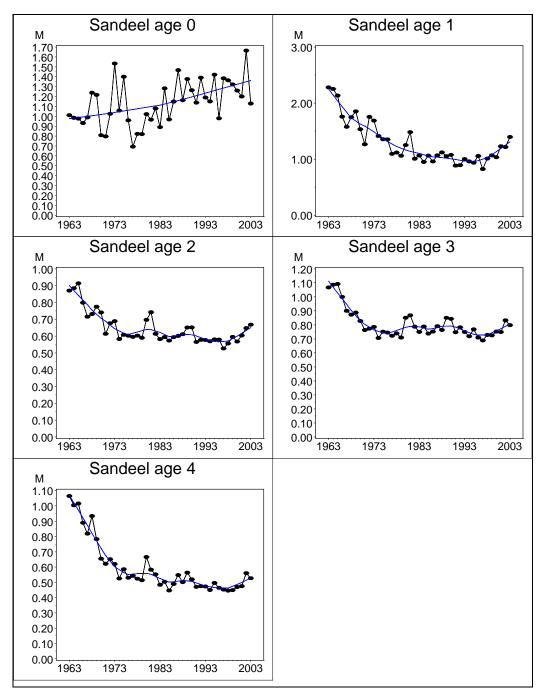


Figure 4.2: Natural mortalities (M1+M2) from MSVPA key-run, estimated values and Loess fitted trend line (cont'd).



 $Figure \ 4.2: \ Natural \ mortalities \ (M1+M2) \ from \ MSVPA \ key-run, \ estimated \ values \ and \ Loess \ fitted \ trend \ line \ (cont'd).$

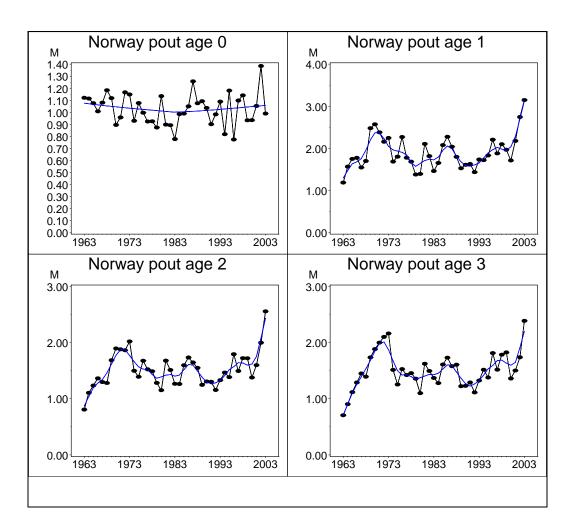


Figure 4.2: Natural mortalities (M1+M2) from MSVPA key-run, estimated values and Loess fitted trend line (cont'd).

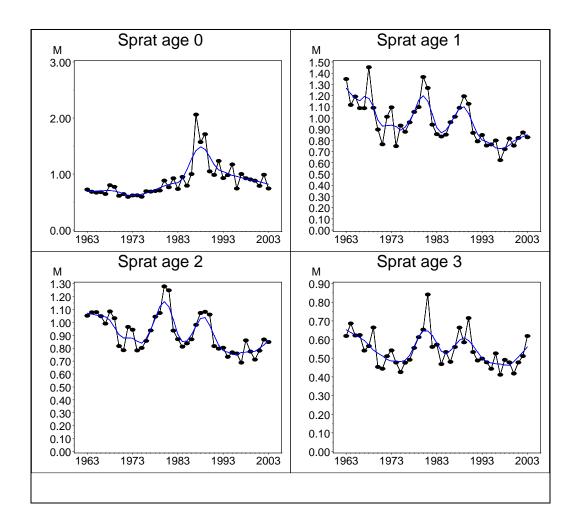


Figure 4.2: Natural mortalities (M1+M2) from MSVPA key-run, estimated values and Loess fitted trend line (cont'd)

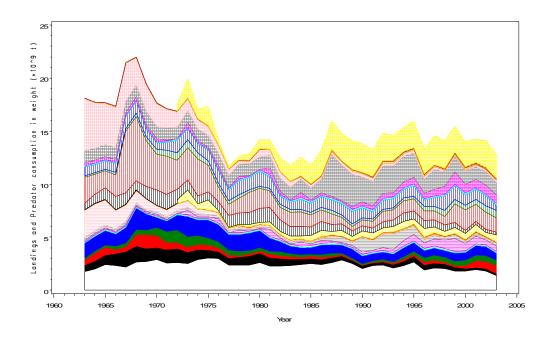
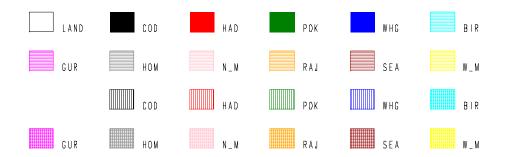


Figure 4.3: Time trends in the biomass of fish landed and consumed by predators; results from the key-run.

Colours indicate the predator species; hatching the status of predator and prey species in MSVPA:

solid: both predator and prey assessed within the MSVPA

horizontal hatching: external predators eating MSVPA-prey wertical hatching: MSVPA predators eating other food external predators eating other food.



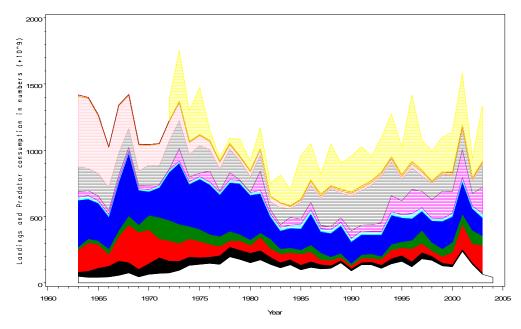


Figure 4.4. Time trends in the <u>numbers</u> of fish landed and consumed by predators; results from the key-run. Legends as in Figure 4.3. Note that predation on other food (vertical and cross hatching in Figure 4.3 is omitted in this figure.

5 Modelling of 0-group fish

The questions of a) whether 0-group fish can be adequately modelled inside the current MSVPA model and b) the importance of modelling 0-group predation mortalities were analysed on the basis of two working papers (Annex 4 and Annex 5). The first working paper focused on the interaction of grey gurnard as an emerging key North Sea predator on 0-group cod and whiting whilst the second working paper addressed these questions more generally. Key results and conclusions of both working papers are presented in this section, followed by comments and conclusions of the Study Group.

5.1 Analysis of the grey gurnard implementation in the North Sea MSVPA

Grey gurnard is a widely distributed demersal species in the North Sea, which frequently ranks amongst the 10 dominant species. Since the late 1980s grey gurnard catch rates in the International Bottom Trawl Surveys (IBTS) showed a pronounced increase and it was included as an "other predator" in the North Sea MSVPA in 1997. During the 2002 ICES Workshop on MSVPA in the North Sea (ICES, 2002) the time series of grey gurnard model input biomass estimates was revised. It was extended in time (1963 - 2001) to cover the observed sharp increase in biomass since the early 1990s.

The 2002 MSVPA run estimated grey gurnard to be responsible for approximately 60% of the total predation mortality on age 0 cod. Within MSVPA, higher mortality rates on the youngest ages leads to higher recruitment estimates, therefore the 2002 run produced a significant positive correlation between the estimate of 0-group cod in quarter 3 and the abundance of grey gurnard at that time. Subsequently, the abundance of 1-group cod in the 1st quarter was weakly but negatively correlated with grey gurnard abundance. The abundances of 0-group cod in the 3rd quarter and 1-group cod in the following 1st quarter were also poorly correlated. However, from field information there was no indication of a higher cod recruitment at age 0 in the 3rd quarter IBTS surveys. Long-term predictions with grey gurnard included in the model frequently led to the extinction of North Sea cod. Subsequently in 2003, it was decided to exclude grey gurnard from the North Sea MSVPA (ICES, 2003) because it was agreed that the current implementation of grey gurnard in the model was not able to adequately describe the quantitative influence of grey gurnard predation on cod populations.

A possible technical reason was discussed as the key mechanism behind the extinction of North Sea cod due to grey gurnard predation: The MSVPA model design with constant suitabilities leads to a Holling Type II functional response (Magnússon, 1995), which means that for a prey stock at low numbers any further slight decrease in prey stock size will result in a non-linear and disproportionally high increase in predation mortality (M2).

The following analysis was designed to specifically assess the following questions:

- 1) Is the combination of the Type II functional response of grey gurnards and the lack of other food responsible for the predicted extinction of cod?
- 2) Does grey gurnard predation affect cod and whiting recruitment?
- 3) Does grey gurnard predation affect the future cod stock recovery potential?

In order to answer the first question, multispecies simulations were conducted to assess the relationship between M2 on cod age 0 and its own abundance. Further, the sensitivity of this M2 to changes in total available prey for cod predators (at the ecosystem scale) was investigated. The second question was addressed by a correlation analysis between independent data sets of cod and whiting recruitment and grey gurnard abundance. The third question was answered by a sensitivity analysis of the impact of grey gurnard abundance and diet composition

on future MSVPA cod stock development. Details on the methods and results can be found in the Annexe 4.

Why does cod go extinct in MSFOR predictions?

The current analysis revealed that the cod extinction in MSFOR predictions was not due to a model artefact: The functional response parameterisation of Holling Type II in the North Sea MSVPA was not responsible for the high 0-group cod predation mortalities at low stock numbers in the 1990s. The cause for cod becoming extinct in the predictions when grey gurnard was included in the model was the combination of low levels of total "available food" between 1999 and 2002 and increasing grey gurnard abundance. It was demonstrated that the predation mortality on 0-group cod was inversely dependent on the amount of total "available food" for all predators preying on cod. The decline in total available food was attributable to declines in the whiting, haddock and herring stocks. Generally, in a multi species model such as 4M which is parameterised with a functional response type II, the rapid decline of a single stock which is small in relation to the total available prey biomass (as is the case for the North Sea cod stock), cannot lead to an over proportionally high increase in predation mortality of its recruits.

The effect of grey gurnard predation on historic cod and whiting recruitment:

Both grey gurnard abundance and cod SSB significantly explained cod recruitment, when used separately. When both were applied in combination grey gurnard lost its significant impact. Cod SSB explained more variability in cod recruitment (approx. 45%) than grey gurnard stock numbers (approx. 30%). Grey gurnard abundances explained over 44% of the total variability in whiting recruitment, much more than whiting SSB was able to explain. When the two independent explaining variables were used together in a single model, both whiting SSB and grey gurnard stock numbers revealed highly significant effects.

In case of the independent whiting and grey gurnard data sets, the full model with both variables explained only 2.3% more than the pure grey gurnard model (46.4%). The different explanatory power of grey gurnard for cod and whiting recruitment can have two reasons: 1) The impact of grey gurnard on cod recruitment was hidden because cod SSB and grey gurnard abundance showed a significant negative correlation. 2) Grey gurnard predation did impact differently on cod and whiting recruitment.

The first possibility cannot be assessed, although whiting SSB was equally negatively correlated with grey gurnard abundance. Potential differences in the interaction processes can be deduced from the ecology of the species: In contrast to whiting, cod is a boreal species for which strong bottom-up effects of temperature and the planktonic environment are known to affect recruitment (Beaugrand et al. 2003, Planque et al. 2003). It is likely, therefore, that the increase in predation rate by grey gurnard on 0-group cod worked simultaneously with increases in fishing pressure and adverse climactic conditions resulting in the decline of the North Sea cod stock. Whereas grey gurnard predation was evidently not a key factor in determining historic cod recruitment, the current analysis demonstrated that this may have changed in recent years and may play a key role for the future cod stock development. A key to understanding the different responses of cod and whiting lies in the spatial distribution of the different life stages of the 3 species: In the 2nd and 3rd quarters, grey gurnards are concentrated in frontal areas in the southern and eastern North Sea, as are small whiting, which in turn led to a significantly higher predator-prey overlap in high density areas of both predator and prey (Floeter et al. 2004a). Small cod had a different spatial distribution, offset from the high density frontal areas of grey gurnard. Hence, for cod the predator-prey overlap was lower and located in areas with lower grey gurnard biomass.

How does grey gurnard predation affect future cod and whiting stock recovery potentials?

Sensitivity tests have shown that only in the prediction scenario with a combination of 50% grey gurnard abundance reduction and 50% stomach content reduction and in the scenario where grey gurnard was excluded, cod SSB was able to exceed B_{lim} (Figure 5.1). In the scenario where grey gurnard was excluded, B_{pa} was almost reached. When grey gurnard was excluded from the model, both cod and whiting stocks increased in the predictions, but the increase in the cod stock was approximately twice that of the whiting stock.

In this context it should be noted that the reason cod was forecast to go extinct whilst whiting remained viable in the MSFOR predictions is that whiting entered the predictions with a much higher SSB. This was due to relatively good year classes in 1997–99, which in turn created high recruitment success in the predictions via the stock-recruitment relationship used. If whiting SSB falls back to low levels it might also be forecast to go extinct in an MSFOR predictions using the same implementation of grey gurnard predation as the 2002 run.

5.1.1 How to proceed with the implementation of grey gurnard in a North Sea multi species assessment model?

An important argument favouring the exclusion of grey gurnard from the MSVPA was that that grey gurnard predation forced model estimates of 3rd quarter recruitment of 0-group cod to be much higher than those indicated by the 3rd quarter IBTS. The majority of predation events occur during the pelagic phase of the 0-group gadoids, which means that the dominant part of the decline in a cod year class takes place before the recruits are caught in the bottom trawl gear of the IBTS. To be able to define a correct implementation of grey gurnards, two key processes need to be understood: 1) Predator - prey overlap between cod, whiting and grey gurnard. 2) The nature of grey gurnard's functional response.

In order to account for the spatio-temporal heterogeneity of the ecosystem, predator-prey overlap indices would have to be explicitly included into the model. The known increase in 2nd quarter temperatures since the early 1990s could have led to an increase in mean length at age of 0-group cod and whiting in the 3rd quarter. This could have led to a reduced time span during which the 0-group gadoids occupied the prey size window suitable for grey gurnard predation and hence led to a reduced predation mortality. Then the positive effect of increased temperature would counter-balance the negative effect of increased grey gurnard abundance. In order to be able to answer these 3 key questions, a new full scale North Sea field program is needed.

In the meantime, the role of grey gurnard in North Sea multi species fisheries assessment should not be further neglected. Instead, alternative scenario predictions with reduced grey gurnard stock numbers and cod and whiting 0-group prey fractions in cod stomachs could help to define boundaries of likely cod and whiting stock projections.

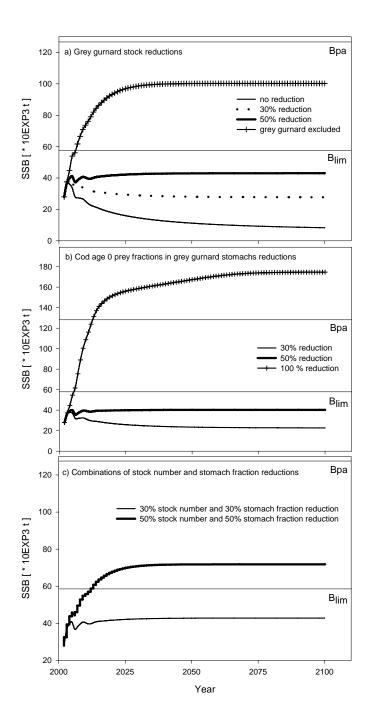


Figure 5.1: Predicted cod spawning stock biomass development from 2002 until 2100. a) with different grey gurnard stock number reductions; b) relative 0-group cod stomach content reductions and c) combinations of both. Cod B_{pa} and B_{lim} reference points are depicted as lines.

5.2 Are we able to model 0-group fish?

Due to differences in recruitment estimates between single species VPA (SSVPA) and MSVPA the question arises which approach captures best the interannual variability of historic recruitment. MSVPA recruitment estimates of 0-group fish depend to a large extent on which stomach data was set used to parameterise the diet selection model (Kempf *et al.* 2003). This is contrary to the assumption of constant suitabilities and increases the uncertainties in 0-group recruitment estimates within MSVPA.

The second question which arises in this context is, whether we are able to model 0-group fish and their highly variable mortality rates with the currently available 4M model. In other words, could the exclusion of 0-group fish from the model lead to more stable model results without loss of important information on inter-annual variations in recruitment?

5.2.1 Methodology

To answer these questions, recruitment estimates (recruitment at age 0 in the 3rd quarter of year t; and recruitment at age 1 in the 1st quarter of year t+1) of different species from four different runs (Single Species, MSVPA keyrun 2003, run 1981 with 1981 stomach data only, run 1991 with 1991 stomach data only) were tested against an index derived from IBTS survey data. Ricker stock- recruitment relationships were fitted for all hindcasts to calculate the explained variance between SSB and recruitment numbers at both defined recruitment dates. For the three MSVPA runs correlation coefficients between age group 1 and age group 0 were calculated to analyse the importance of the modelled 0-group fish predation mortalities for recruitment success. In prediction runs with different stomach data sets (stomach data 1981 or 1991) the importance of the variability in suitability coefficients between 1981 and 1991 on future stock development was also analysed. Finally the predictive power of multi species and single species approaches for generating recruitment estimates was tested by making a time series split analysis.

A detailed description of material and methods can be found in annex 5.

5.2.2 Key results

5.2.2.1 Performance of different model approaches to hindcast recruitment strength and to establish Ricker stock-recruitment relationships

Correlations between anomalies (differences from mean recruitment) in VPA recruitment and anomalies in the IBTS index were of a similar strength in multi species and single species runs, with some exceptions for age 0 recruits (herring and whiting with higher Pearson correlation coefficients in the single species run). The Pearson correlation coefficients for age 0 recruits were low for most species (<0.4). Markedly higher correlation coefficients (>0.6) were calculated for age 1 recruits.

Differences in fitted stock-recruitment curves were pronounced especially between run 91 and the other model approaches. Much higher age 0 recruitment numbers were calculated with run 91 for most species. The slope at the origin as well as the overall shape of the curves were different. For age 1 recruits the stock-recruitment curves of the four runs were more similar to each other than for age 0 recruits, especially for cod.

The differences in r^2 between Ricker stock recruitment curves fitted for age 0 and age 1 recruits were small in all runs and for most species. Only for whiting and haddock a higher r^2 for age 0 recruits was obtained. In general the relationship between SSB and recruits was slightly better in the MSVPA approaches than in the single species calculations. However, in general for most species r^2 was low (<0.4) in all runs.

5.2.2.2 Importance of 0-group predation mortalities

The correlation between age 0 and age 1 anomalies was of differing strength in the three MSVPA runs. In run 2003 and run 81, age 1 anomalies were highly correlated with age 0 anomalies (Pearson correlation coefficients of 0.921** or 0.952** respectively) the correlation was much weaker in run 91 (0.511**). This means that in run 91 the 0-group predation mortalities had the potential to alter the recruitment success of incoming year classes to a large

extent. Strong age 0 year classes could turn into weak recruitment years for age 1 after the 3rd and 4th quarter 0-group predation mortalities were applied and vice versa.

The observed differences in recruitment relationships and predation pressures between run 81 and 91 translated into different predicted SSB estimates in mid-term forecasts (Figure 5.2). Differences in predation pressures, caused by different sets of suitability coefficients (resulting from the different stomach data sets), and determined the future stock development. As an example whiting went extinct when the 1991 stomach data set was employed, regardless which stock-recruitment relationship was used. When the 1981 stomach data set was used, SSB was stable or even increased until 2010 (again regardless of which stock-recruitment relationship was used). The recovery potential of cod was also highly determined by the choice of the stomach data set.

5.2.2.3 Performance in predicting recruitment

The predictability of recruitment in the time series split analysis turned out to be weak in all model approaches. Furthermore, the correlation between predicted recruitment anomalies and IBTS index anomalies between 1992 and 2001 were negatively correlated in 13 out of 24 cases for predictions of age 0 quarter 3 recruits. The performance when predicting recruitment at age 1 in the 1st quarter was slightly better but all correlation coefficients were under 0.4 and not significant.

5.2.3 Conclusions

In comparison to the single species approach, the modelling of 0-group predation mortalities in the multi species 4M runs was not able to improve the correlations between modelled recruit numbers and the corresponding IBTS indices. The modelled age 1 recruits showed a better correlation with the IBTS index. However, whether the ability to model recruitment at age 1 is higher than for 0-group recruits or whether the weaker correlation between the 0-group IBTS index and age 0 recruits is caused by the low catchability of 0-group fish in the 3rd quarter IBTS, remains unclear.

When single species and multi species VPA models were compared, taking multi species interactions explicitly into account did not decrease the variance of the fitted Ricker stock-recruitment curves. Furthermore, the precision of recruitment predictions could not be improved by including 0-group fish dynamics. However, future stock development at a given fishing mortality and stock-recruitment relationship was strongly determined by the predation pressure on 0-group fish in the model (Figure 5.1). Thus excluding the 0-group would mean loosing an important process determining recruitment success. In the current 4M model, a large part of the inter-annual variability in predation pressure are ignored by assuming constant suitabilities and ignoring differences between the stomach data years 1981 and 1991. For this reason the MSVPA diet selection model must be improved by implementing process models that take inter-annual changes in predation more realistically into account. Further, the development of enhanced stock-recruitment relationships which are not solely based on SSB is needed to increase recruitment predictions also in multi species models.

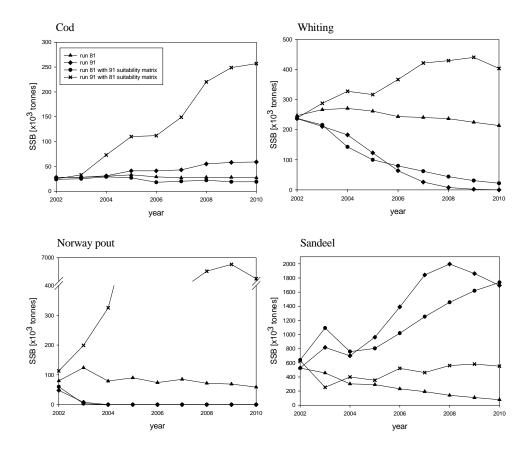


Figure 5.1: Predicted SSB development under different combinations of input data from the respective MSVPA results and assumed future predation mortalities derived from different suitability matrices.

5.3 Comments of the SG on whether 0-group fish can adequately be modelled using the 4M or other multispecies modelling approaches

Based on the two baseline WDs and subsequent discussions, the SG agreed that:

- Post-larval 0-group fish can be modelled using 4M.
- due to the lack of suitable field data on absolute numbers and trends of 0-group fish there is currently no way of ground-truthing the resulting 0-group numbers.
- in order to be able to ground-truth the recruitment numbers resulting from MSVPA, more reliable 0-group survey indices would be required as the 3rd quarter IBTS 0-group indices are unreliable due to a low and variable catchability. The required field evidence would also need to cover the pelagic phase of 0-group gadoids as a large share of the predation on 0-group fish takes place during this phase.
- the differences between the suitability matrices resulting from the 1981 and 1991 stomach data set affect the perceived 0-group dynamics most strongly. Consequently, the current use of stomach data sets where stomach samples are aggregated over all available data years means that inter-annual changes in predation pressure are not taken into account.
- in the current 4M model setup, the course of the medium term stock projections are determined by the choice of the stomach data set rather than the shape of the relationship between spawning stock and recruitment.
- as the most recent stomach data originate from 1991, the drastic changes in the North Sea ecosystem in terms of predator and prey stock sizes and spatial distribution since 1991 are not reflected in the current model run. In particular, the increase in grey gurnard combined with the decline in cod is expected to have changed the predatorprey overlap between both species. In addition, the recent decline in sandeel, another important prey of grey gurnard, is likely to have has changed the diet composition of this species.
- to adequately model the impact of predation on survival of 0-group fish in recent years, new stomach data reflecting the current state of the ecosystem are required.

The SG also discussed the relevance of modelling 0-group fish more generally, in order to provide a reliable multi-species assessment:

- the modelling of 0-groups in the hindcast model runs, has little effect on the older age classes.
- for short term projections the modelling of 0-group fish is relatively unimportant.
- The 0-groups are, however, an important food source for the MSVPA predators and make up around 75% of the total fish consumption in the model (Figure 5.2).
- By excluding 0-group from the model, they would have to be included as 'other food' which implies that the biomass of 0-group fish would be assumed constant. This would mean that the appearance of a large year class would have no effect on the modelled consumption of other food, and more importantly would be have no effect on the estimate of predation on older age groups.
- the shape and absolute levels of the Stock Recruitment Relationships (SRRs) resulting from the MSVPA hindcasts are different when 0-group fish are modelled (re-

- cruitment at age 0 in quarter 3) compared to when the model starts with age 1 fish. However, the quality of the SRRs in terms of explained variance does not differ.
- predation on 0-group fish in the third and fourth quarter of their first year of life has the potential to deteriorate the correlation between numbers at age 0 in quarter 3 and numbers at age 1 in the first quarter of the next year, i.e., recruitment strength is not determined at age 0 in the beginning of the 3rd quarter but rather during the entire first year of life.
- one of the initial objectives of the North Sea multi species assessment WG was to improve the SSRs by taking multi species effects into account. This objective could not be met, as the interannual variability in the currently modelled processes determining predation on 0-group fish (e.g., spatial predator-prey overlap) is not sufficiently implemented in the current model design.
- for reliable medium-, and long term stock projections (including stock recovery scenarios), an adequate implementation of 0-group fish survival rates is a key requirement.
- to be able to provide reliable medium,- and long term multi species stock projections
 as well as multi species reference points, the long term objective of the multi species
 work in ICES must be to strive to an enhanced implementation of the 0-group fish
 dynamics, which requires:
 - a more reliable estimate of the biomass of key predators of 0-group fish, in particular seabirds, mackerel, horse mackerel and grey gurnards;
 - a more reliable implementation of the key predators of 0-group fish, which refers especially to dominant pelagic piscivores (mackerel, horse mackerel) but also new emerging predators;
 - the development and implementation of enhanced process models affecting recruitment and survival rates of 0-group fish;
 - ultimately, the closing of the life cycles in the forecast models.
- In the final conclusion the SG agreed that there is still a long way to go until 0-group fish dynamics can be reliably modelled in multi species models. However, the SG also agreed that their is no alternative to it, given the ever increasing demand for medium-, and long term fisheries management under the umbrella of the precautionary approach to fisheries management.

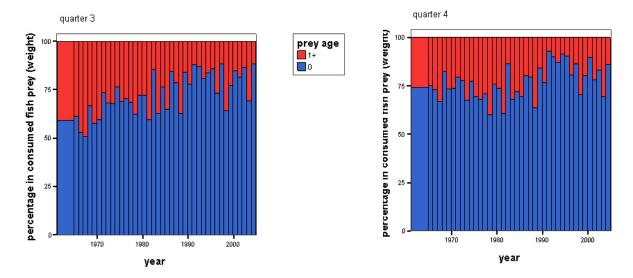


Figure 5.2: Percentage of 0-group and older fish in consumed fish prey of all modelled predators in the system.

6 Progress in Ecopath with Ecosim modelling of the North Sea ecosystem

6.1 General approach

Trophic models based on Ecopath with Ecosim (EwE) methodology are widely used for the quantification of food webs and analyses of ecosystem dynamics (Christensen *et al.* 2000). The approach is founded on a static description of the ecosystem assuming mass-balance between production, mortality and metabolic losses. Biological species are aggregated into functional groups linked through the consumption matrix. The model also allows dynamic simulations in time and space, as well as fitting to time-series, and evaluation of fisheries management scenarios.

The EwE approach is relatively simple to apply and provides a broad perspective for ecosystem analyses. It includes functional groups, which are not routinely assessed by working groups and helps to evaluate their importance for the system. Information assimilated and outputs from the model (e.g., various ecosystem indicators, Cury *et al.* 2005) can provide input for other multispecies and ecosystem models and related analyses. EwE is used as a common platform for comparative ecosystem analyses and several EwE models have already been built in the ICES area (e.g., North Sea, Barents Sea, Baltic, and English Channel), others are under construction (Irish and Celtic Seas).

Our objective was to use the most relevant information available in the North Sea area (stock assessments, diet, consumption) to build a comprehensive model that will be used as a tool for ecosystem and fisheries analyses. We chose 1991 as the year to model the North Sea, so that we could use the extensive database from the 1991 stomach sampling project (Hislop 1997), and because assessment and survey data for the period 1991–2003 could be used for model fitting. Also, 1991 is the only year for which international fisheries data are available, disaggregated into different fleet and gear components (from STECF).

The model will be reviewed by competent peers e.g., specialists in taxonomic groups and specific methods, that will integrate relevant expertise and help correct errors; refining parameters and providing advise on improvements.

6.2 Model construction

The model has 71 functional groups including 3 mammal, 1 seabird, 47 fish, 14 invertebrate, 4 autotroph, and 3 export (detritus +discard) groups. The commercially important commercial fish species were divided into juvenile and adult groups (e.g., cod, whiting, herring). Several fish species, which are also commercially and/or functionally important, were represented as single species or family groups (e.g., hake, dab, gurnards). Other species are included in aggregated groups based on similar taxonomic or functional characteristics e.g., large and small gadoids, large and small demersals, and pelagic fish. The model was supplied with new estimates of biomass, production and consumption rates and diet composition compiled from ICES and UK databases. Information on commercially important fishes was largely based on ICES stock assessments (mainly from MSVPA). The biomass of ~80 fish species monitored by the IBTS, which are not subject to regular stock assessment, was estimated following the approach of Sparholt (1990). The diet matrix was compiled using 1991 year of stomach data (Hislop et al. 1996) and other literature sources. Fisheries landings were derived from the data compiled by ICES, and discards of 39 different fishing fleets were compiled from the ICES fisheries statistics database, 1991 Scientific Technical Committee for Fisheries (STECF) data, UK Fishing activity database and Trio Discards database (CEFAS) (ICES, 2002, Mickleburgh 2003).

6.3 Comparative analyses

Comparative analyses of input parameters have been performed aiming to: 1. Check parameter consistency; 2. Detect direction of changes relative to previous work. The results are still preliminary and more confidence might be assigned to them after balancing the model, testing parameter sensitivity, and fitting to time-series.

In terms of total consumption the most important groups are small flatfishes, clupeids and sandeels. The most important fish predators are gadoids, mackerel/horse mackerel, and gurnards. Minke whales, porpoises, rays and megrim also emerge as important predators together with seals and seabirds. The most important fish preys are gadoids, clupeids and sandeels.

Biomass estimates were compared to historical data (Sparholt, 1990; Mackinson, 2002). Total fish biomass in the North Sea was estimated at ~26 million tons by the late 19th century (Mackinson, 2002) and ~ 10 million tons in 1991 (present study). The greatest change was in exploited target species e.g., cod, haddock, saithe, herring and flatfish. There was also an important decrease in cetaceans, seabirds and elasmobranches, but an increase in seals in 1991 compared to the 1880s. Decrease was less significant in mackerel, sandeel and prey fish. Biomass estimates in the 1880s model were based on scarce data and heavy assumptions; consequently they should be interpreted with a great deal of caution. The total fish biomass does not appear to change considerably between the early 1980s and early 1990s; however there were changes in relative importance of different stocks. Elasmobranches, gadoids, horse mackerel, and large demersal fish have decreased, but clupeids, gurnards and prey fish increased in 1991 compared to 1980s.

6.4 Input from the Study Group

The work of the SG contributed to revising/refining of some of the parameters in the present version of 1991 EwE model. Revised and new data and results from the M4 key-run will be used for improving the input parameters. These include new consumption estimates (mack-

erel, horse mackerel, seals, saithe), new data of abundance and consumption of seabirds. New methods for estimation of consumption, based on limited data will be kindly provided by Dr Axel Temming, and used for improving consumption estimates in several fish species.

Future work will include balancing the present draft model, fitting to time-series of biomass and fishing effort and further applications with simulation of alternative fishing and environmental change scenarios.

7 Recommendations and further work

7.1 The future of multispecies research in ICES

7.1.1 The need for multispecies stock assessment within ICES

The Ecosystem Approach to management has achieved substantial attention in recent years and the focus on the effect of fishing on non-target species has increased. Predatory species may experience decreased growth or reproductive success if food abundance is diminished through fishing and prey items may substantially increase when released from predation pressure through the removal of larger predators. The work of the Study Group on Multispecies Assessment in the North Sea has shown that non-target species such as the grey gurnard may have a profound effect on the ecosystem and may inhibit the return of former key predators such as cod (ICES, 2003). Furthermore, it has been shown that multispecies estimates of recovery potentials under specific harvest control rules differ substantially from those estimated in a single species context. The Study Group has furthermore produced estimates of the relative importance of the removal of each prey by different predators and the fishery which have provided a basis to evaluate the degree to which a reduction in prey density is fishery induced. ICES currently do not have other working groups or study groups capable of answering these questions for the North Sea.

Lately, both ICES and the EU have been changing the focus of management plans from short term plans to long term plans with short term implications. The single species target reference points of such long term plans depend entirely on the assumption of constant natural mortality. Studies have shown that reference points are far from constant if this assumption is replaced by an estimate of predation mortality (Gislason 1999, Collie *et al.* 2003, ICES, 2003). Hence the target reference points derived in single species analyses do not necessarily reflect the value of the target points in a multi-species context and the basis for the reference point (i.e., maximum sustainable yield) may not even exist in a single species sense when multispecies interactions are taken into account.

7.1.2 Strategy for multispecies stock assessment and advice on management issues

The future task for multispecies research will be to build a toolbox for evaluating management goals in a multispecies context, for example tools to evaluate the effect on top predators and non-target species of removing important prey such as sandeel. Evaluation of recovery plans and the effect of climatic changes on species interactions should be a focus within the models. For example, a change in temperature will affect consumption, growth, migration and predator-prey overlap, and hence species interactions, but it has also led to the appearance of 'new' warm water species in the North Sea, e.g., red mullet and sea bass. The estimation of the effect of these 'new' species and changes to distributions of existing species on predator-prey interactions requires a multispecies model.

Currently, most of the scientific work on multispecies interactions takes place in projects outside ICES and therefore ICES needs a forum for the integration of this external research into

its advisory procedures Projects funded by the EU exist in most sea areas and include the Bay of Biscay, Nordic Seas and Baltic as well as the North Sea. This makes the existence of a permanent Working Group on Multispecies Assessment particularly important as there is a need to coordinate multispecies research within the ICES area and provide a forum for the exchange of ideas on the future research on multispecies models. Multispecies issues are by definition long term issues. The collection of new data is time consuming as is obtaining data from other working groups. Both of these arguments support the existence of a Working Group on Multispecies Assessment. The work conducted by a Working Group on Multispecies Assessment falls under the remit of ACFM as the models basically provide advice on total allowable catch or other management measures. Though the models may also in the future provide advice on the effect of different management regimes on non-target species, this will be the effect under the assumption of a range of different fishing patterns rather than a full population model for these species.

The research in the Working Group on Multispecies Assessment should not be confined to a single modelling approach but should cover a range of alternative models of multispecies interactions. The group will therefore encourage the participation of scientists working with multispecies models not currently represented in any existing Study Group. Furthermore, as ICES does not have dedicated working groups on multispecies interactions, the Working Group on Multispecies Assessment will provide a forum for the discussion and implementation of multispecies models in all ICES areas.

The Study Group on Multispecies Assessment in the North Sea proposes that the Working Group on Multispecies Assessment should meet annually. Every third meeting should be dedicated to constructing an updated key run with new catch data. The intervening years should be used to work on specific themes, drawing in expertise from other scientific disciplines and from outside the ICES community. In these years, new runs will be based on the same input data as the latest key run but underlying process models may be changed or new species added. Alternatively the WG could meet annually for key or update model runs and run in conjunction with a series of themed workshops.

An important task of the future Working Group will be to initiate the collection of new data and the collation of existing data into a format than can be used in the model. The last large scale exercise on dietary composition of fish in the North Sea was conducted in 1991. Extrapolation from these data to the current time and further into the future is a risky strategy. For example the emergence of gurnards as a major influence on the future of the cod and whiting stocks has highlighted the uncertainty of reliance on data 15 years old. The Study Group on Multispecies Assessment in the North Sea believes that the predictions of multispecies models will not be reliable if diet composition data are not collected on a recurring basis, in particular under the current changing climatic conditions. Such data could be collected efficiently during existing monitoring surveys. The study group feels that the lack of new stomach data is currently the greatest source of uncertainty in the model and therefore agreed that the theme of the first meeting should be to investigate and describe the exact characteristics (statistical and geographic) of the required stomach samples. In years after 2005, the Working Group on Multispecies Assessment proposes to address the following themes:

- Investigate and describe the exact characteristics (statistical, spatial and temporal) of a stomach sampling exercise (2006);
- 2) Investigate the decline in forage fish and the effects of this on species interactions and top predators (2007);
- 3) Incorporate spatial aspects and changes in predator-prey overlap (based on results from EU-funded BECAUSE)(2008);
- 4) Estimate the limit values of the biomass of other stocks which allow recovery of different species under a variety of climatic regimes (based on results from EU-funded UNCOVER) (2009);
- 5) Estimate multispecies reference points under different exploitation schemes (2010).

7.1.3 Future terms of reference

The **Working Group on Multispecies Assessment** [WGMSA] (Chair: Ewen Bell, UK and Morten Winther, Denmark) will meet at ICES Headquarters in early 2006 for 6 days to:

- a) review the value of existing stomach data currently not available to the Study Group for the estimation of species interactions;
- b) determine the characteristics of a stomach sampling program necessary to achieve a certain statistical and geographic precision of diet composition and food selection for different predators, to be identified by the Working Group;
- c) design a stomach sampling programme based on the results from ToR b);
- d) update population estimates for gurnards, horse mackerel, seabirds (WGSE) and marine mammals (WGMME) and diet composition estimates for seabirds (WGSE) and marine mammals (WGMME).

WGMSA will report by xxx 2006 for the attention of the ACFM (who will be parent).

Supporting information

Priority:	Multispecies assement modelling is essential for the development of viable long-term management strategies
Scientific Justification and relation to action plan:	The ICES Multispecies Assessment Working Group (MAWG) was disbanded in 1997 but in 2003, the Study Group on Multispecies Assessment in the North Sea (SGMSNS) was formed. The Study Group was tasked with producing an updated key-run of the North Sea MSVPA and attempting to identify the future direction of multispecies work in the North Sea.
	The focus on the ecosystem approach to management and long term management strategies has not decreased since the formation of the study group and neither has the need to provide an estimate of the effect of targeted fishing on non-target species. Lately, ICES has changed the focus of the management plans from short term plans to long term plans with short term implications. Such long term plans depend entirely on the knowledge of species interactions and hence the SGMSNS considers that a Working Group on Multispecies Assessment should be formed. The Working group should meet annually and the SGMSNS proposes a first meeting in early 2006.
Links to Action Points:	1.1, 1.2, 3.3, 3.2, 3.5, 3.6, 3.13, 4.1, 4.2, 4.11, 4.15
Resource Requirements:	
Participants:	Approx 20. Expertise in ecosystem, modelling and fish stock assessment.
Secretariat Facilities:	
Financial:	No financial implications
Linkage to Advisory Committees:	ACE, ACFM
Linkage to other Comities or groups:	PGNSP, NORSEPP, REGNS
Linkages to other organisations:	
Secretariat	

Marginal Cost	
Share:	

8 Request for data

Contingent on the establishment of a Working Group on Multispecies Assessment, the requirements from other ICES Working Groups for multispecies assessment modelling in the North Sea are:

- 1) From the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK) quarterly catches and mean weight at age by year and age group of sole, plaice, Norway pout, sandeel, cod, haddock, whiting and saithe including discards and unreported landings if these are used for the final assessment presented by the Working Group are requested;
- 2) From the Herring Assessment Working Group for the Area South of 62° N (HAWG) quarterly catches and mean weight at age by year and age group of herring and sprat used for the final assessment of the Working Group are requested;
- 3) From the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (WGMHSA), the numbers and weight at age of mackerel and horse mackerel of each age present in ICES area IV in each quarter and year are requested;
- 4) From the Working Group on Marine Mammal Ecology (WGMME), population numbers and diets of marine mammals in ICES area IV, by year and quarter have been part of the ToR for the last two years. When this request has been fulfilled the Working Group needs updates of population numbers when available;
- 5) From the Working Group on Seabird Ecology (WGSE), population numbers and diets of seabirds in ICES area IV, by year and quarter have been part of the ToR for the last two years. When this request has been fulfilled the Working Group needs updates of population numbers when available.

The Study Group would like to stress that the quarterly catches for haddock, cod, whiting and saithe have not been delivered by the WGNSSK for the last two years and this lack of data introduces the need to assume an unchanged quarterly catch distribution. This is not satisfactory.

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Annex 3: The feasibility of including harbour porpoise *Phocoena phocoena* as a predator in MSVPA

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ABSTRACT

In 2003 SGMSNS examined the possibility of including cetacean data within MSVPA. At the time both SGMSNS and WGMME were pessimistic about the availability of relevant information, however subsequently useful data on harbour porpoise has recently emerged (or will appear in 2005), and this body of new work might make it possible to include a cetacean species for the first time (next year).

In this working-paper we review the information currently available (population abundance, long-term trends, food consumption estimates, diet composition) and we propose some initial estimates. It is thought that harbour porpoise numbers have increased in the North Sea in recent years following a period of sustained decline during the 1970s and 1980s. The favoured prey of harbour porpoise appears to be whiting, sandeel, cod, haddock and sole, all of which are commercially important species included in MSVPA.

The North Sea porpoise population may exceed 229 196 animals, or 9649 tones. Assuming an average consumption rate of around 3.5 kg per day, then porpoises will remove in excess of 290 000 tones of fish every year.

INTRODUCTION

Term of Reference (ToR) c) for SGMSNS in 2005 is to: "incorporate the biomass data, consumption rates and diet compositions provided by the Working Group on Seabird Ecology and the Working Group on Marine Mammal Ecology for marine mammals and seabirds. Evaluate the importance of newly introduced predators (e.g., harbour seals), and whether these affect 4M outputs".

In 2003 SGMSNS examined the possibility of including cetacean data within MSVPA (ICES, 2003). At the time both SGMSNS and WGMME were pessimistic about the availability of relevant information, however subsequently useful data on harbour porpoise has recently emerged (or will appear in 2005), and this body of new work might make it possible to include a cetacean species for the first time (next year). The harbour or common porpoise (*Phocoena phocoena*) is the smallest but by far the most numerous of the cetaceans found in north-west European continental shelf waters. The status of small cetaceans, and particularly harbour porpoise has been a cause of concern for many years. This concern has stemmed from substantial incidental catches in fishing operations (e.g., Vinther 1999), apparent declines in the number of animals stranded or sited in coastal waters, and possible risks from contaminants. There is a clear need for basic information on the biology of *P. phocoena* and other small cetaceans, including a more cohesive assessment of their current abundance, long-term population trends and the role that these species play as predators of commercially important fish species.

In 1987 Sparholt provided an overview of natural mortality estimates ('M2' values) for commercial species included within MSVPA. He also provided estimates of natural mortality which could be ascribed to predation by fish, mammal and bird species not included in MSVPA (a component of 'M1' residual-mortality values). Sparholt's (1987) estimate of the amount of fish (MSVPA species) removed by marine mammals each year amounted to only 78000 tonnes. This now seems to be a gross underestimation since grey-seals (47 600 individuals) on their own, have been estimated to consume in excess of 146 000 tones of fish each year (SGMSNS estimate for 2000) and harbour porpoises (229 196 individuals) may account for a further 290 000 tonnes.

Harbour Porpoise Abundance

The need for accurate and precise estimates of abundance of *P. phocoena* and other small cetaceans throughout the North Sea and adjacent waters has been recognized by the UN Convention on the Conservation of Migratory Species (Bonn Convention), through its Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS); the European Union, through its Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora; the UN Environment Programme, through its Global Plan of Action for Cetaceans; the International Council for the Exploration of the Sea (ICES); the North Sea Ministerial Conference; and the International Whaling Commission (IWC). The latter specifically recommended that *P. phocoena* abundance should be estimated using dedicated sightings surveys in the North and Baltic Seas (IWC 1992). Project SCANS (small cetacean abundance in the North Sea and adjacent waters) was initiated in 1993 to fulfil this need (Hammond *et al.* 2002).

The project involved an intensive shipboard and aerial survey using line transect sampling. Shipboard transects covered 20 000 km in an area of 890 000 km2. Aerial transects covered 7000 km in an area of 150 000 km2. The survey area was stratified into blocks on the basis of logistical constraints and taking account of existing information on cetacean distribution and relative abundance. Abundance estimates included corrections for sea-state and school/pod size (see Hammond *et al.* 2002). The SCANS survey is due to be repeated in 2005.

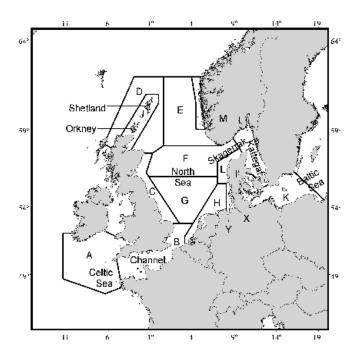


Figure 1. Area covered during the SCANS survey in 1994. Blocks A–I were surveyed by ship. Blocks I' (a subset of block I), J–M, X and Y were surveyed by aircraft (from Hammond *et al.* 2002).

Table 1: Estimate of harbour porpoise abundance in areas of the North Sea, according to the SCANS survey carried out in summer 1994 (from Hammond *et al.* 2002).

AREA CODE	DESCRIPTION	Km² (and % of area)	ESTIMATED ABUN- DANCE (CV)	ESTIMATED DEN- SITY
В	Channel	105 223	0	-
С	UK East Coast	43 744	16 939 (0.18)	0.387
D	North of Scotland	102 277	37 144 (0.25)	0.363
Е	Northern North Sea	109 026	31 419 (0.49)	0.288
F	Central North Sea (North)	118 985	92 340 (0.25)	0.776
G	Central North Sea (South)	113 741	38 616 (0.34)	0.340
Н	Dutch Coast	45 515	4 211 (0.29)	0.095
J	Shetland and Orkney	31 059	24 335 (0.34)	0.784
L	Danish Coast	18 176	11 870 (0.47)	0.635
M	Norwegian Coast	12 612	5 666 (0.27)	0.449
	Total	700 358	262 540	

ICES Area IV (North Sea) covers 611 408 km². The scaled estimate of abundance for ICES area IV is 229 196 individuals (in 1994).

Long-term population trends

Information on the present and past abundance of harbour porpoise in the North Sea, beyond Hammond *et al.*'s estimate for 1994, is extremely limited. However, most studies from the early 1990's suggested population decline, particularly in the southern North Sea and the English Channel (Reijnders and Lankester 1990; Reijnders 1992).

From the 1940s onwards, reports had suggested that porpoises were becoming increasingly scarce in France (Duguy, 1977), Belgium (De Smet 1974), The Netherlands (Verwey 1975; Verwey and Wolff 1981, Addink and Smeenk 1999), Germany (Schultz 1970; Benke *et al.* 1998) and Denmark (Andersen, 1982). The picture was slightly different for UK waters where sightings indicated a decline in the English Channel after the early 1960's, but no convincing evidence for a decline along English North Sea Coasts (Evans 1980, Evans 1990a, Northridge and Lankester 1990, Kayes 1985). Only after the early 1980's was a decline apparent for the Northern North Sea (Evans 1987).

The status of the North Sea harbour porpoise population in recent years is somewhat uncertain, however there are some indications that the population may now be increasing (ICES, 2004). The situation should be clarified in 2005 when the SCANS survey is to be repeated.

Trends in occurrence of porpoises off the coast of the Netherlands have recently been reported by C.J. Camphuysen (http://home.planet.nl/~camphuys/Bruinvis.html) based on incidental sightings and systematic surveys. It would seem that there has been an increase in the sighting rate of harbour porpoises that started in the late 1980s and continued to 2004 (Figure 2). Similarly for certain sites around the UK, porpoise sightings seem to be increasing (Figure 3 and 4) or at least, no longer decreasing (Evans *et al.* 2003).

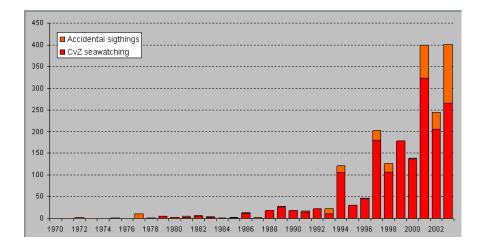


Figure 2: Harbour Porpoises reported from coastal sites in The Netherlands since 1970 (http://home.planet.nl/~camphuys/Bruinvis.htm, updated 3/1/2004)

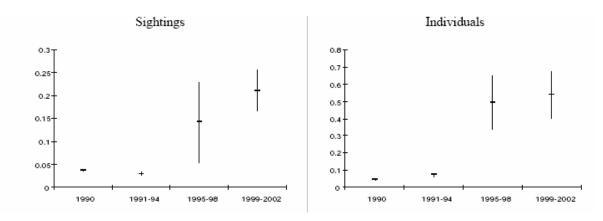


Figure 3: Harbour Porpoises reported from coastal sites in Eastern Scotland since 1980 (Effort-related Observations). Values are mean numbers of sightings and individuals per unit effort, with 95% confidence limits (from Evans *et al.* 2003). Other regions have insufficient effort data for analysis of long-term trends: however, in Eastern England, sightings and individual rates are much higher in 1998–2002 than for previous years.

In the Shetland Islands (north Scotland), declines in porpoise numbers were observed between 1982 and 1990 (Figure 4), followed by an increase, at least in the southern part of Shetland between 1990 and 1995 (Evans *et al.*, 1997). Changes in harbour porpoise abundance were related to annual variation in sand-eel populations. Sand-eel spawning stock biomass declined markedly from 1984–92, when coastal summer porpoise populations also apparently declined. During 1993 and 1994, sand-eel spawning stock biomass was relatively high and harbour porpoise abundance was also higher (Evans *et al.*, 1997).

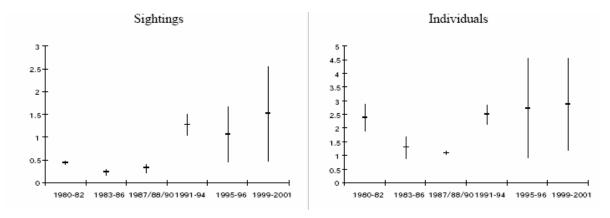


Figure 4: Harbour Porpoises reported from coastal sites in Northern Scotland (including Shetland and Orkney) since 1980 (Effort-related Observations). Values are mean numbers of sightings and individuals per unit effort, with 95% confidence limits (from Evans *et al.* 2003).

As a corollary of this suggested increase in porpoise numbers over the past 10 years, porpoise strandings along the Belgian coast have increased markedly (Figure 5). A similar increase may have been observed along parts of the North Sea coast of the UK (Richard C. Sabin, UK Cetacean Strandings Coordinator, Personal Communication).

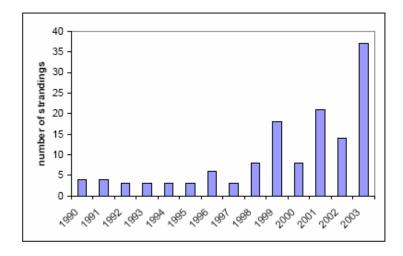


Figure 5: Number of harbour porpoise strandings on Belgian coasts, 1990 to 2003 (From ICES 2004).

Whether or not the increase in the number of stranded animals reflects a 'real' increase in the size of the underlying population, or simply a change in fishing practices leading to additional mortality, remains a matter of conjecture. However, an observer programme recording incidental capture of harbour porpoise in the Danish set-net fishery has suggested that levels of porpoise bycatch (and hence the level of fishing mortality inflicted on the population) has decreased over the past 10 years, from 7366 individuals in 1994 to only 3887 individuals in 2001 (Vinther and Larsen 2002, reported in Stenson 2003). Similarly, an observer programme focusing on UK cod, sole, skate and turbot set-net fisheries has indicated a decline in porpoise bycatch from 818 individuals in 1995 to 436 individuals in 1999, which has coincided with a decrease in fishing effort (see Stenson 2003).

For this first (rough) attempt at producing MSVPA input data on harbour porpoise, we might apply a 6% year-on-year increase in North Sea abundance after the SCANS 1994 estimate, and a slow (0.5% per year) decline in numbers prior to 1994 (Figure 6). Very little has been published on the maximal population growth rate of harbour porpoises, however Caswell *et al.* 1998 suggested a range of 5–10% per year for animals in the Gulf of Maine, taking into account age at sexual maturity, age-specific fertility and age-specific survival (Lockyer 2003). Barlow and Hannan (1995) suggested that the maximal rate of population growth for animals off California is 9.4% per year, and an analyses of models of east coast Canada and US porpoises considered a theoretical maximum of 10% per year (NOAA 1994).

Recent developments in numerical techniques such as 'dynamic-factor-analysis' (Zuur *et al.* 2003) could be used as a more rigorous method of re-constructing a single time series of abundance estimates for porpoises in the North Sea. This method looks for common trends in a wide range locally-derived time-series such as those illustrated in Figures 2–5. Component time-series are standardized (and therefore unitless) and it is possible to examine whether the underlying trends observed correlate with explanatory variables such as sea surface temperature or food availability. The unitless time-series resulting from 'dynamic-factor-analysis' could be scaled in accordance with the one-off SCANS surveys of 1994 and also the new data which will emerge as a result of the new SCANS survey in 2005.

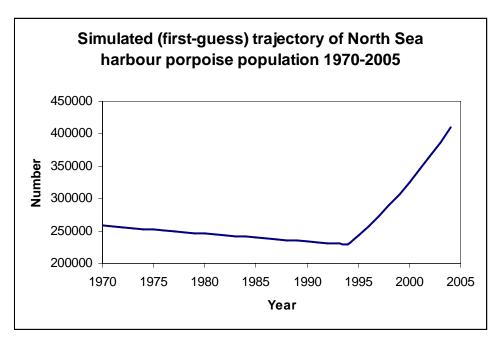


Figure 6: A first (rough) attempt at producing MSVPA input data on harbour porpoise, assuming a 6% year-on-year increase in North Sea abundance after the SCANS 1994 estimate (229 196 individuals), and a slow (0.5% per year) decline in numbers prior to 1994.

Estimation of prey consumption

It has not been possible to relate the weight of prey represented by the remains in harbour porpoise stomachs to a rate of prey consumption. However, consumption can be estimated by scaling the amount of energy represented by remains in a sample of stomachs to the amount of energy required to sustain the estimated number of porpoise in an area for the length of the season under consideration.

If p^{E_j} is the proportion, by energy value, of each species in the diet; E_j is the energy density of each species; N is the estimated number of porpoise days in the area during the quarter; and R is the porpoise daily energy requirement, then total consumption, C_j , by weight, of each species is:

$$C_i = p^E_i NR/E_i$$
.

Values of fish energy density used in the calculations are given in Appendix 1. Estimates of porpoise numbers are given in Table 1 (229 196 individuals). Worthy *et al.* (1987) provided one estimate of the average daily energy requirement for harbour porpoise; **3213** Kcals.d (Active Metabolic Rate 155.7 W, 3 porpoises, average mass 35.2 kg; 13 452 kJ.d⁻¹). Boyd (xxxx) proposed a relationship between the body mass of various marine mammal species and the 'Field metabolic rate' (the metabolic rate measured in free-ranging animals):

FMR =
$$30.43 \text{ Mass}^{0.524}$$
 $r^2 = 0.86.$

If we accept that the mean length of animals in the North Sea is 138.3 cm (based on 63 stranding records reported in Law (1994), excluding all individuals of age 0) and that the relationship between animal body mass and length is:

Mass =
$$0.000081*$$
Length ^{2.67}

(Lockyer and Kinze 2003), then average mass is 42.1 kg and FMR is 216.1W. This equates to 18 668 kJ.d⁻¹ or **4458.5** Kcals.d⁻¹.

Lockyer *et al.* (2003) examined the growth, energy utilization and food intake of two harbour porpoise individuals held in captivity (a male weighing 37.5 - 44.75 kg, a female weighing 40.5 – 51.6 kg). Food intake was recorded daily and the diet comprised mainly herring with some mackerel, (and minor amounts of cod, whiting, blue whiting and trout). The energy density of these fish species is high, ranging from 5.24 to 7.89 kJ g⁻¹ wet weight of fish. Food intake fluctuated seasonally, and daily food consumption in both animals represented about 7.1 to 9.5% of body weight, which equates to approximately 2.9 - 4.3 kg of fish or 19 842 – 29 416 kJ (4739 - 7025 kCal).

Yasui and Gaskin (1986) constructed an energy budget for wild harbour porpoise in the Bay of Fundy, Canada. These authors estimated a daily energy intake (for a 53kg animal) of 3005 kCal. This would equate to 3.5% of total body weight per day, which is considerably less than that reported for animals in captivity (e.g., Lockyer *et al.* 2003; Andersen 1965; Heel 1962). Kastelein *et al.* (1997) recorded food consumption in captivity (based on six individuals) to range between 4 and 9.5% of body weight. Santos (1998) used the more conservative estimate of 3.5% and population estimates from the 1994 SCANS survey to calculate the amount of prey removed each year by harbour porpoises in Scottish, Danish and Dutch waters.

Several authors have noted that the average consumption rate increased during summer months (e.g., Lockyer *et al.* 2003; Andersen 1965; Heel 1962), and this should be taken into account when developing realistic input values for MSVPA.

Diet Composition

On several occasions diet composition has been estimated in the literature as the proportion by weight, of each prey species in the diet (see Table 2). In each case, fish weights were estimated from otolith or cephalopod beak measurements, using standard regressions (e.g., Härkönen 1986). Each author produced length-frequency distributions (see Figures 7 and 8) and then converted these to weight-frequency distributions using standard weight-length relationships (e.g., Coull *et al.*, 1989; Bedford *et al.* 1986; Dorel 1986). This weight or length-stratified data could be readily used to produce age-stratified input data for MSVPA.

To apportion estimated consumption of each prey species into age classes, the consumption of species j in age class a, C_{ja} is estimated as:

$$C_{ja} = \frac{\sum_{l} W_{jl} p_{jla}}{\sum_{l} W_{jl}} C_{j},$$

where W_{il} = the estimated weight of species j in length class l (from sample data),

 p_{ila} = the proportion of species j in length class l in age class a (from age-length keys),

 C_i = the estimated consumption of species j.

The C_{ja} estimates are then summed over areas to give estimates for the entire North Sea for each quarter.

Table 2: Overall diet composition estimates (% wet weight) for harbour porpoise in the North Sea (ICES area IV) and Skagerrak (ICES area IIIa).

PREY SPECIES	GERMAN BIGHT	KATTEGAT AND SKAGERRAK	SCOTTISH WATERS	
	Benke <i>et al</i> . (1998)	Börjesson <i>et al</i> . (2003)	Santos et al. (2004)	
	1990–1994	1988–1996	1992–2003	
Cod	6.2	4.9	0.59	
Haddock	0	0.2	1.36	
Saithe	0	4.4	6.13 ^b	
Whiting	8.9	4.8	51.73	
Pout	0	3.6	3.69	
Sandeel	36.6	1.6	24.79	
Dover Sole	27	0	0	
Plaice	0	0	0	
Herring	0	49.9	1.42	
Sprat	0	8.0	0.35	
Mackerel	0	0	1.5	
Horse-mackerel	0	0	0.01	
Other	21.3	22.7ª	8.43°	
N (number of stomachs)	61	112	188	

aincludes 'unspecified gadoids' (6.1%); bunspecified 'haddock/saithe/pollack'; 'includes 'unidentified Gadidae' (3.37%) and 'unidentified Clupeidae' (0.43%).

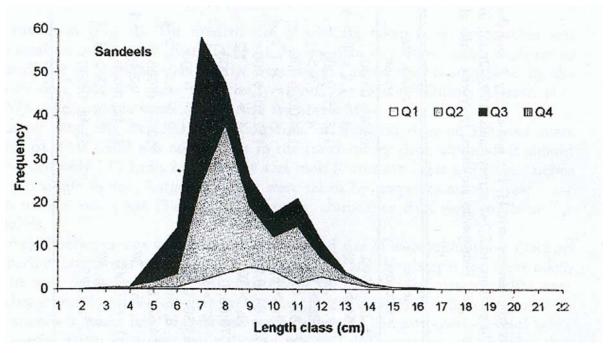


Figure 7: Length-frequency distribution (by season) of sandeels eaten by porpoises, using combined data for 1992–2003 (from Santos et al., 2003).

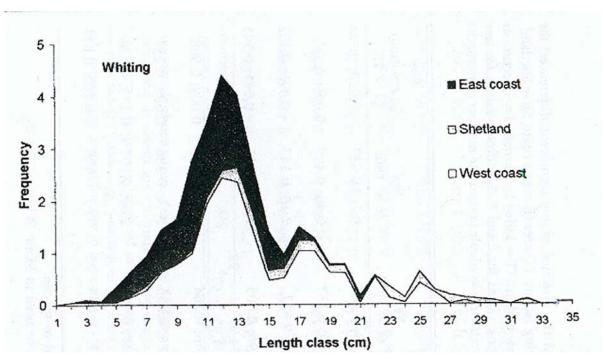


Figure 8: Length-frequency distribution (by geographic area) of whiting eaten by porpoises, using combined data for 1992–2003 (from Santos *et al.*, 2003).

On the basis of analyses conducted on stranded animals, Santos *et al.* (2004) has suggested that whiting and sandeels are the most important prey for porpoises around the coasts of Scotland, comprising around 80% of the diet. The next most important prey categories were the gadid groups haddock/saith/pollacj and *Trisopterus* spp. (*T. Esmarkii* and *T. Minutus*). Other MSVPA fish species present in smaller numbers included cod, herring, sprat, mackerel and horse mackerel.

The first detailed studies on harbour porpoise diet in eastern North Atlantic were carried out by Rae (1965, 1973), who found herring, sprat and whiting to be the main prey in Scotland during 1959–1971. Martin (1996) found that gadids (whiting, haddock, Norway pout and pollack) sandeels and gobies were the most important prey (by weight) for porpoises in UK waters in recent years. Taken together, these published data suggest that porpoise diets have changed significantly over the last four decades. There has been speculation about the likelihhod and consequences of porpoises **switching to other prey species** if their main prey were depleted by overfishing (IWC 1996; Santos and Pierce 2003). Indeed Smeenk (1987) suggested that the decline in herring stocks might have caused the (apparent) decline of harbour porpoises in most European waters during the 1970s. Evans *et al.* (1997) postulated that changes in harbour porpoise abundance during the 1980 might be related to annual variation in sand-eel populations since sand-eel spawning stock biomass declined markedly from 1984–92, when coastal summer porpoise populations also apparently declined.

Aarefjord *et al.* (1995) found herring to be the most important prey in Scandinavian waters, with other important prey differing between Norwegian waters (saithe, blue-whiting, capelin) and the Danish North Sea and Baltic (cod, whiting, sand-eels, gobies). Börjesson *et al.* (2003) found herring to be the main prey in the Swedish Skagerrak and Kattegat Seas (see Table 2). In German waters, sand-eels and common sole were the most important prey (Benke *et al.* 1998; Table 2).

CONCLUSIONS

Several important advances have been made since the 2003 SGMSNS meeting and it would now almost certainly possible to provide sufficient input data to add harbour porpoises to the North Sea MSVPA model. In 2005 a second SCANS survey will be conducted and taken together with 1994 survey, a relative time series of abundance estimates might be generated and scaled to these 'realistic' values.

Two important documents were published in 2003/2004: an 'Atlas of Cetacean Distribution in North west European Waters (Reid *et al.* 2003) and a 'UK Cetacean Status Review' (Evans *et al.* 2003). The data described in these documents (and others) include local time-series of porpoise sightings and strandings. One **recommendation** of this working-paper is that, as a matter of some urgency, an attempt be made to collate these local data-series and construct a single time series of abundance estimates using newly-available numerical techniques such as 'dynamic-factor-analysis'. Such a time series would prove invaluable in the long-term as marine-mammal population status is to be used as an important Ecological Quality Objective (EcoQO) for management by OSPAR and the 'North Sea Conference'.

Seasonally and geographically resolved porpoise stomach contents data have recently been published by Santos *et al.* (2004). This data (together with scaled data from elsewhere) could be readily and easily used to generate input data for MSVPA, and to fit 'suitability' curves.

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Annex 4: An analysis of the grey gurnard implementation in the North Sea MSVPA

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Abstract

Grey gurnard is a widely distributed demersal species in the North Sea, which has been ranked frequently under the 10 dominant species. Since the late 1980s grey gurnard catch rates in the International Bottom Trawl Surveys (IBTS) showed a pronounced increase and it was included as an "other predator" in the North Sea Multi Species Virtual Population Analysis (MSVPA) in 1997. The MSVPA results estimated grey gurnard to be responsible for approximately 60% of the total predation mortality on age 0 cod. Long-term MSVPA predictions led to the extinction of North Sea cod and subsequently in 2003 grey gurnard was excluded from the North Sea MSVPA. As a possible technical reason the Holling Type II functional response (FR) implemented in the model was discussed. In the current analysis it was demonstrated that the Holling Type II FR was not responsible for the extinction of cod in the model, which was rather a true effect of high grey gurnard predation. Further it was shown that grey gurnard predation had a significant top-down effect on whiting (Merlangius merlangus) and potentially also on cod (Gadus morhua) recruitment, which was linked to the spatial distribution of the three species. Eventually, the implications of the results for North Sea cod stock recovery plans were discussed:

Introduction

Grey gurnard (*Eutrigla gurnadus*), is a widely distributed demersal species in the North Sea, which has been ranked under the 10 dominant species (Yang 1982; Daan *et al.* 1990). Since the late 1980s North Sea grey gurnard catch rates in the International Bottom Trawl Surveys (IBTS) showed a pronounced increase (ICES, 2002). Possibly grey gurnad was able to occupy substantial parts of the ecological niche freed by the diminishing demersal gadoids, especially after the regime shift in the late 1980s (Reid *et al.*, 2001a,b; Beaugrand *et al.*, 2003). Grey gurnard shows a clear seasonal shift in distribution, in winter it concentrates in the western part of the central North Sea, whereas these concentrations disperse in spring and summer (Knijn *et al.* 1993). The quarterly IBTS in the North Sea revealed that in quarter 2 and quarter 3 larger sized grey gurnard predominantly occur in high abundances along the 50 m depth contour, as well as at the Doggerbank, the Fisher Banks, off Jutland and in the German Bight (Heessen and Daan 1994).

The most extensive description of grey gurnard diets originate from the multi-national sampling efforts under the auspices of International Council for the Exploration of the Sea (ICES) during the second year-of-the-stomach in 1991, when grey gurnard was included in the stomach sampling program as a priority by-catch species (de Gee and Kikkert 1993). The dominant results of this analysis were, first that grey gurnard fed mainly on juvenile fish of which a high proportion were commercially exploited gadoids, and second that the ontogenetic diet shift from an invertebrate-dominated to a fish-dominated diet occurred at rather small sizes of approximately 20 cm. The mean percentage of cod and whiting in the stomach contents of grey gurnard larger than 30 cm ranged between 18% and 32%, depending on the season. The overall mean percentage of gadoid prey weights in the stomachs of grey gurnard larger than 20 cm was 37%, with 52%, 30%, 34% and 30% in the four quarters. These figures are underestimates, because the prey category "other fish" also included all fish prey items that were not identified at the genus or species level. Approximately 90% of cod (Gadus morhua, and 60% of whiting (Merlangius merlangus)) found in all grey gurnard stomachs were smaller than 10 cm. A more detailed description of the diet composition is provided by (de Gee and Kikkert 1993). Already in the early 1990s, Heessen and Daan (1994) concluded that grey gurnard may play an important role in the North Sea ecosystem.

As the 1991 stomach sampling program revealed the significant consumption of commercial fish species by grey gurnard, it was included as an "other predator" in the North Sea Multi Species Virtual Population Analysis in 1997 (MSVPA, ICES, 1997). The historic stock trends of "other predators" are not calculated inside the model but are rather given as an external model input. The role of "other predators" in the MSVPA is to prey on dynamically implemented species such as e.g., cod and whiting. The parameterisation of the grey gurnard feeding interactions in the North Sea MSVPA is based on a total of 6486 stomachs with food, sampled in 4 quarters in 1991.

During the 2002 ICES Workshop on MSVPA in the North Sea (ICES, 2002) the time series of grey gurnard model input biomass estimates was revised. It was extended in time (1963 - 2001) to cover the observed sharp increase in biomass since the early 1990s. The MSVPA results estimated grey gurnard to be responsible for approximately 60% of the total predation mortality on age 0 cod. However, the inclusion of grey gurnard in the 4M (North Sea MSVPA) model suite (Vinther *et al.* 2002) led to unsatisfactory model performance as specifically the estimates of cod year-class strength became driven by gurnard abundance and long-term predictions frequently led to the extinction of North Sea cod. Subsequently in 2003, it was decided to exclude grey gurnard from the North Sea MSVPA (ICES, 2003) because it was agreed that the current implementation of grey gurnard in the model was not able to describe the quantitative influence of grey gurnard predation on cod realistically.

A possible technical reason was discussed as the key mechanism behind the extinction of North Sea cod due to grey gurnard predation: The MSVPA model design with constant suitabilities leads to a Holling Type II functional response (Magnússon, 1995), which means that for a prey stock at low numbers any further slight decrease in prey stock size will result in a non-linear and unproportionally high increase in predation mortality (M2).

The currently highly uncertain impact of grey gurnard as predator of commercial species in the North Sea generated the motivation for the current analysis, which was designed to specifically assess the following questions: (1) Is the North Sea MSVPA Type II functional response parameterisation of feeding interactions responsible for the extinction of cod due to grey gurnard predation? (2) Does grey gurnard predation affect cod and whiting recruitment? and (3) Does grey gurnard predation affect the future cod stock recovery potential?

In order to answer the first question multispecies simulations were conducted to assess the relationship between cod age 0 M2 and its own abundance. Further, the sensitivity of cod age 0 M2 to changes in total available prey for cod predators on the ecosystem scale was investigated. The second question was addressed by a correlation analysis between independent data sets of cod and whiting recruitment and grey gurnard abundance. Generalised Linear Models (GLM) were employed to explain historic cod and whiting recruitment variability as a function of spawning stock biomass (SSB) and grey gurnard abundance.

The third question was answered by a sensitivity analysis of the impact of grey gurnard abundance and diet composition on future MSVPA cod stock development.

Materials and methods

Multi species model setup

Virtual Population Analysis (VPA) calculations and predictions for ICES area IV (North Sea) was carried out using the computer program 4M (Vinther *et al.*, 2002). The model was parameterised using the 2003 North Sea MSVPA keyrun data (ICES, 2003). A MSVPA hindcast model run including the typical predator and prey species in the North Sea (Table 1) was carried out identical to the keyrun in 2003, with grey gurnard additionally included as an "other predator".

In addition to the MSVPA hindcast, a prediction run with the forecast model MSFOR was carried out, using F_{pa} (F precautionary; ICES, 2003b) as future fishing mortality and results (Ricker type stock-recruitment relationships, initial stock numbers) from the MSVPA hindcast as input. This enabled the possibility to examine the Holling Type II effect on cod stock development for future years up to the extinction of cod.

Table 1: Classification of Multi Species Virtual Population Analysis (MSVPA) species as predator and prey

Only predator	Predator and prey	Only prey
Saithe (Pollachius virens)	Cod	Herring
North Sea mackerel (Scomber scombrus)	(Gadus morhua)	(Clupea harangus)
Western mackerel (Scomber scombrus)	Whiting	Sprat
Grey gurnard (Eutrigla gurnadus)	(Merlangius merlangus)	(Sprattus sprattus)
Starry ray (Raja radiata)	Haddock	Norway pout
Grey seal (Halichoerus grypus)	(Melanogrammus aeglefinus)	(Trisopterus esmarkii)
Sea birds		Sandeel
Horse mackerel (Trachurus trachurus)		(Ammodytes marinus)

A time series of gurnard population numbers was constructed by the MSVPA Study Group (ICES, 2002) from IBTS data. This included trawl catch-per-unit-of-effort (CPUE) data from quarter 1 in the period 1966-2001 and catch data from all quarters in 1991-1997. Early data sets where grey gurnard was completely absent were omitted from the analysis. The remaining hauls (N = 14 600) were analysed using a Generalised Linear Model (GLM), by assuming a Poisson distribution and a log-link function. Year, quarter, gear and roundfish area were deployed as explanatory variables of the numbers caught by size class. The use of a Poisson distribution did allow for zero observations without additional model assumptions, while assigning less weight to zero and near-zero observations. The size classes (< 10 cm; 10 - 20 cm; 20 -30 cm, and \geq 30 cm) matched those used for the stomach content information in the MSVPA. For simplicity, these size classes are referred to as age classes 0 - 3 in the following. With the exception of the model for the smallest size category, which did not converge, most factors investigated contributed significantly. The GLM model estimates of year and quarter effects were used to construct the time series of grey gurnard stock numbers by assuming an average biomass of 205 000 t over the entire period. This figure was taken from Daan et al. (1990) who calculated average grey gurnard biomass from English Groundfish Survey (1977–1986) data, assuming a gadoid-type availability.

Assessing the relationship between calculated predation mortality and cod age 0 abundance (Analysis 1)

The aim of analysis 1 was to examine the role of Holling Type II functional response, i.e., the increase in 0-group cod M2 due to decreasing cod abundance, in a multi species environment. This could not be done by using real MSVPA model runs, because changes in 0-group cod M2 caused by changes in predator abundance over time cannot be distinguished from the Holling Type II functional response effect. The isolated Holling Type II effect can only be assessed when the predator field (abundance, species and age composition) is constant. Hence, model results from the MSVPA and prediction (MSFOR) were used to externally calculate the effect of the Holling Type II functional response on the predation mortality of a declining cod stock. The current approach can be seen as a simulation, analysing the Holling Type II effect in a multi species environment under boundary conditions that resemble the North Sea MSVPA model setup.

Predation mortalities of 0-group cod in the third and fourth quarter of the last MSVPA year (2001) were calculated for simulated recruitment values of cod (N). These calculations were done applying the MSVPA Equations 2–4 (Sparre 1991) to the constant year 2001 stock sizes of all other predator and prey species and age classes, only the abundance of 0-group cod was varied. It was assessed how much the 2001 predation mortality for 0-group cod varied when the predator field of 2001 was simulated to prey on different third quarter average cod age 0 recruit abundances (N). This approach ensured that all simulated "available food" (i.e., prey biomass multiplied by suitabilities (Equation 2)) variations and hence M2 changes were solely caused by 0-group cod abundance changes, i.e., the isolated Holling Type II effect.

The simulated 0-group cod recruitment ranged from highest estimated MSVPA recruitment numbers in the year 1981 down to an artificially low recruitment of only one million 0-group cod, mimicking a recruitment close to the extinction of cod. The increase in M2 with declining cod recruitment numbers was plotted to show the range of possible M2 variations caused by constant predator stocks but decreasing 0-group cod numbers in an otherwise constant prey field.

$$(1) N = N^{\circ} \cdot \frac{(1 - e^{-z})}{z}$$

(2) Available
$$[s,a,y,q,p,j] = N_{[s,a,y,q]} \cdot wp_{[s,a,y,q,p,j]} \cdot Suit_{[s,a,q,p,j]}$$

(3)

$$Available_{[p,j,y,q]} = \sum_{i=1}^{NoS+1} \sum_{b=0}^{NoA(i)} N_{[i,y,q,b]} \bullet wp_{[i,y,q,b,p,j]} \bullet Suit_{[i,q,b,p,j]}$$

(4)
$$M2_{[s,a,y,q,p,j]} = \frac{N_{[p,j,y,q]} \cdot r_{[p,j,q]} \cdot Suit_{[s,a,p,j,q]}}{Available_{[p,j,y,q]}}$$

where: N° = stock numbers at the beginning of a quarter, N = quarterly average stock numbers; Z = total mortality; Available = available food, s = prey species; a = prey age; y = year; q = quarter; p = predator species; j = predator age, wp = mean prey weight; Suit = suitability coefficient, r = ration; M2 = predation mortality. Equation 2 represents the prey (s, a) biomass available to a predator (p, j). Equation 3 represents the total available biomass of all prey types to a predator (p, j). Equation 4 represents the predation mortality of prey (s, a) due to the consumption of predator (p, j) in a certain year and quarter (y, q) and is the extension of the single species predation mortality equation (prey consumed per time unit divided by average prey stock per time unit) to the multi species situation (see e.g., Sparre 1991, Magnússon 1995 for the derivation).

Assessing the relationship between calculated M2 and "available food" variations (Analysis 2)

Variations in 0-group cod predation mortality caused by the Holling Type II effect depend in a multispecies context on both: Changes of 0-group cod abundance itself and changes in the total available food for every predator which preys on cod (see Equation 4). Whereas the previous analysis examined the isolated cod abundance changes, this analysis takes changes in the entire prey field into account.

By applying the extracted prey abundances, total mortalities and suitabilities from the MSVPA and MSFOR runs to equations 1–3, "available food" was calculated for the third and fourth quarter for each of the years 1974 to 2020 for every predator species and predator age class preying on 0-group cod. Thus, the original time series of historic and predicted available food was extracted from the converged MSVPA and MSFOR model runs.

The predator stock situation of 2001 was then chosen as the constant reference predator field. Using this constant predator field, the third and fourth quarter 0-group cod predation mortalities in 2001 were calculated using the 47 different "available food" values from the time series (Equation 4). This analysis examined the dependence of cod age 0 predation mortality on the

status of the North Sea ecosystem with respect to the total available prey biomass. It enabled to show the Holling Type II effect on 0-group cod M2s together with the effect of variable amounts of other available prey in the full MSVPA model environment. The constant predator field was simulated to feed upon different historic and predicted prey fields. Translated into the real North Sea ecosystem this was a way to assess the effects of changes in absolute abundances of prey stocks, and subsequent changes in the quality of total prey biomass, for the total cod age 0 predation mortality. For example, the recent decline in Norway pout (*Trisopterus esmarkii*) and sandeels and the increase in herring (*Clupea harengus*) stocks changes the predation level on cod, as all these potential prey species have different predator-specific accessibilities and are differently "liked to be eaten" by predators. Therefore, it was possible to assess whether the observed fast M2 increase of 0-group cod through grey gurnard predation in the MSVPA 2002 keyrun during the 1990s was predominantly caused by the Holling Type II effect, which then must have been driven by decreasing "available food" over time.

In order to be able to visualize the dependence of total 0-group cod M2 in 2001 on variable amounts of "available food" variability in a single plot, weighted average "available food" values over all predators and predator age groups preying on 0-group cod were calculated for the third and fourth quarters of the 47 years from 1974 to 2020. The proportional contribution of every predator species and predator age group to the total predation mortality of cod age 0 was chosen as the weighting factor. This was necessary because in the model every predator has its specific set of suitability coefficients and hence "available food" and creates a partial M2 for 0-group cod, which have to be summed over all predator species and ages to give the total M2.

Historic cod and whiting recruitment variability (Analysis 3)

Generally, a higher 0-group M2 caused by increasing predator stock sizes will lead to a higher estimated recruitment in the backward working MSVPA (ICES, 2003). This resulted in a clear positive correlation between the cod 0-group M2 and the abundance of grey gurnard (ICES, 2002). In the current analysis, the abundance of 1-group cod and whiting estimated in a MSVPA without grey gurnard was correlated with the abundance of grey gurnard. Hence, as in the present analysis grey gurnard abundance and cod and whiting abundance estimates originated from independent information sources, the correlation provides a hint for an underlying biological process at work. For a more clear presentation of the results, the yearly anomalies were taken instead of absolute stock numbers. The anomalies were calculated as the ratio of the annual stock numbers at age and the mean stock numbers at age over the entire time period. After a descriptive visualisation a correlation analysis (using Pearsons correlation coefficient r) between the subsequently calculated natural logarithms of cod and whiting age 1 stock number anomalies and the natural logarithms of stock number anomalies of age 3 grey gurnards in the third quarter of the previous years was conducted. Under the hypothesis that gurnard predation had an impact on cod and whiting recruitment, a negative correlation between the independent data sets of cod recruitment at age 1 and the abundance of large gurnards at the time when the gadoid juveniles are in their late pelagic and settlement phase could be expected.

Generalised linear models (GLM, using MathSoft S-Plus[™] 2000) were fitted to explain the 1st quarter cod and whiting age 1 stock numbers as a function of grey gurnard abundance in the previous years and cod and whiting spawning stock biomasses (Table 2). By using a Type III sums-of-squares (SSQ) the SSQs for each term listed in the ANOVA table were adjusted for all other terms in the model. These sum of squares are independent of the order that the terms are specified in the equation. Finally, it was tested whether it made a difference when the dependent data sets were used instead of the independent data sets: The same GLM's were fitted, but the cod and whiting age 1 stock numbers were derived from the MSVPA keyrun in 2003 with grey gurnard included as "other predator".

Sensitivity of the cod stock predictions to grey gurnard's relative stomach content of_cod age 0 prey and grey gurnard abundance (Analysis 4)

Predictions using the MSFOR module of 4M were carried out on the basis of a set of MSVPAs where both the relative stomach contents of 0-group cod in the 1991 grey gurnard stomach data set and the stock abundance of gurnards were artificially reduced by 30%, 50%, 70%, 100% relative to the observed values.

Table 2: Generalised linear models of the following form were fitted:

(Explained variable ~ Variable 1 + Variable 2, family: Gaussian, link: Identity). Note that each model had two versions: Version A: The cod (*Gadus morhua*) and whiting (*Merlangius merlangus*) stock numbers originated from the Multi Species Virtual Population Analysis (MSVPA) keyrun in 2003 without grey gurnard (*Eutrigla gurnadus*). Version B: the cod and whiting stock numbers originated from the 2003 MSVPA keyrun but with grey gurnard included. SSB: spawning stock biomass.

Model No.	Explained variable	Variable 1	Variable 2
1 A 1 B	log (N), cod, age 1, in quarter 1, year = x	log (N), grey gurnard age 3 anomaly, in quarter 3, year = x -1	
2 A 2 B	log(N), cod, age 1, in quarter 1, $year = x$	log (SSB), cod, in quarter 1, year = x -1	
3 A 3 B	log (N), cod, age 1, in quarter 1, year = x	log (SSB), cod, in quarter 1, year = x -1	log(N), grey gurnard age 3, in quarter 3, year = $x - 1$
4 A 4 B	log (N), whiting, age 1, in quarter 1, year = x	log (N), grey gurnard age 3 anomaly, in quarter 3, year = x -1	
5 A 5 B	log(N), whiting, age 1, in quarter 1, year = x	log (SSB), whiting, in quarter 1, year = $x - 1$	
6 A 6 B	log(N), whiting, age 1, in quarter 1, year = x	log (SSB), whiting, in quarter 1, year = $x - 1$	log(N), grey gurnard age 3, in quarter 3, year = $x - 1$

To test any second order effects grey gurnard was also totally excluded and the results were contrasted with those from a 100% reduction of relative stomach contents. This approach mimics for example a decrease in spatial overlap between gurnard and cod due to a shrinking in the realized cod habitat due to, e.g., a decrease in stock size and the recent temperature increase. This would most likely reduce the share of cod in the gurnard's diet and other prey species would be consumed more, including juveniles of species that feed on cod as adults, as e.g., whiting.

Also predictions with different combinations of reduced 0-group cod relative stomach contents and reduced grey gurnard abundances were performed. In all predictions and for all fish stocks single species F_{pa} for ICES area IV (ICES, 2003b) were assumed as future fishing mortalities. All other options and input parameters were identical to the MSVPA keyrun in 2003 (ICES, 2003).

Results

Assessing the relationship between calculated predation mortality and cod age 0 abundance (Analysis 1)

As expected when using a model which follows Holling Type II, the cod age group 0 predation mortality in 2001 increased with decreasing cod recruitment numbers (N, Figure 1). The lowest annual 0-group cod predation mortality ($M2_{year} = M2_{3rd \text{ quarter}} + M2_{4th \text{ quarter}} = 3.43$) caused by the predator field of 2001 resulted from the combination of the highest observed MSVPA cod recruitment (in 1981) with the "available food" of the year 2001. The highest

2001 0-group cod predation mortality ($M2_{year} = 4.0$) was calculated at the lowest cod recruitment numbers. The difference between the annual 0-group cod predation mortality in the last year of the hindcast (2001) and at the (artificially) lowest third quarter recruitment numbers ($N = 1 \cdot 10^6$) was only $M2_{delta} = 0.11$ (from $M2_{year} = 3.89$ to $M2_{year} = 4.0$).

The relative overall increase in M2 calculated for the range of the simulated values (2001 to N = $1 \cdot 10^6$) was only 30% higher than that calculated from the observed period (1981 to 2001). This means that any further slight decrease in 0-group cod stock numbers beyond the low 2001 stock situation resulted not in an unproportionally high increase in predation mortality. This can also be seen in absolute terms, as the increase over the whole range was already rather small (M2_{delta} = 0.11, see above).

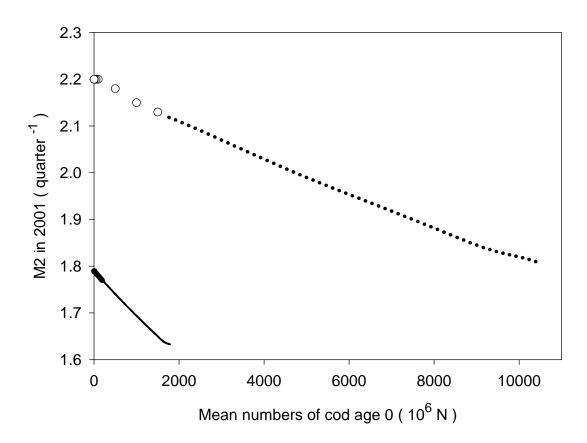


Figure 1: Dependence of calculated cod (*Gadus morhua*) 0-group M2 on cod recruitment numbers. Depicted is the range of cod 0-group M2s resulting from the highest observed Multi Species Virtual Population Analysis (MSVPA) cod recruitment (in 1981) to the (artificially) lowest third quarter recruitment numbers (N =1•10⁶). •: Quarter 3, MSVPA cod numbers. O: Quarter 3, artificially reduced cod numbers. : Quarter 4, MSVPA cod numbers. : Quarter 4, artificially reduced cod numbers.

Assessing the relationship between calculated M2 and "available food" variations (Analysis 2)

After looking at the isolated effect of historic cod recruitment variations on cod age 0 predation mortality, the whole variability in total "available food" for all predators preying on cod age 0 was taken into account: the annual predation mortality of the year 2001 created by the constant 2001 predator field varied from $M2_{year} = 2.87$ to $M2_{year} = 4.56$ over the complete range of variations in "available food" from 1974 to 2020 (Figure 2). So, the relative changes in M2 were much larger than those calculated solely from variations in cod recruitment (Figure 1).

This relationship between the annual predation mortality in 2001 and historic and predicted "available food" situations (and therefore the Holling Type II effect in the multi species model context) can also be displayed as a time series: The M2 caused by all predators (from the 2001 MSVPA predator field) preying on 0-group cod are compared with the M2 created only by grey gurnard (2001 biomass) preying on 0-group cod (Figure 3).

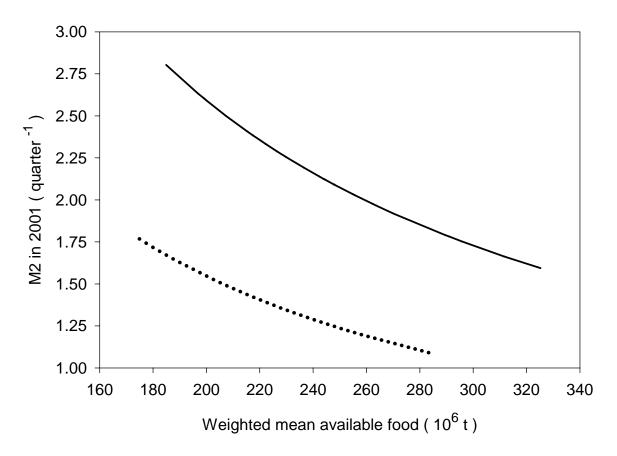


Figure 2: Dependence of calculated cod (*Gadus morhua*) 0-group M2 in 2001 on weighted mean "available food" (from 1974 to 2020) for the 2001 Multi Species Virtual Population Analysis (MSVPA) predator field (restricted to predators that preyed on cod). Quarter 3: solid line, quarter 4 dotted line.

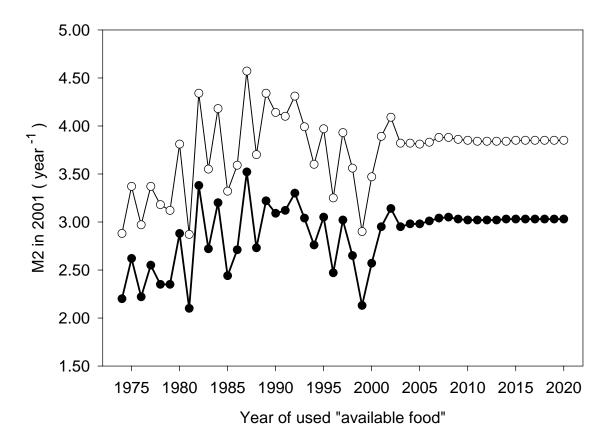


Figure 3: Dependence of the calculated 0-group cod (*Gadus morhua*) M2 in 2001 on the annual "available food" situations. The 0-group cod predation mortality in 2001 was calculated from 47 simulations where the constant predator stocks of 2001 preyed on each of the different "available food" situations between 1974 to 2020. O: M2 caused by all predators combined. •: M2 caused by grey gurnard alone.

The calculated 2001 M2_{year} values for both predator groups showed very similar trends. From the plot grey gurnard can be identified as the main predator for 0-group cod in the model. Because of the highly correlated curves of predation mortality exerted by both predator groups (Pearson correlation coefficient r=0.984, p<0.001), the "available food" variations over time for grey gurnard and other predators preying on cod age 0 were obviously very similar.

From the graphs it can be deduced in which direction and to what extend the functional response Type II parameterisation in the MSVPA prey selection model influenced the historic and predicted 0-group cod M2 values. Even though, the absolute M2 values have no real meaning since they are theoretical values for the reference predator field in the year 2001: The Holling Type II functional response parameterisation in 4M caused relatively low annual predation mortalities of age 0 cod when historic "available food" prey fields of the late 1970s were combined with the 2001 predator field. However, the "available food" of the 1980s and early 1990s resulted in rather high mortalities, with a maximum in 1987. Calculations with the "available food" prey fields from the period 1992 to 1999 showed a decreasing trend in 0-group cod 2001 annual M2's. This matched with an increase in weighted mean "available food" for predators preying on 0-group cod between 1992 and 1999 in the third and fourth quarters (Figure 4).

The sharp increase in cod age 0 predation mortality resulting from the simulations with the 1999 to 2002 prey fields (Figure 3) coincided with a sharp decline in weighted mean "available food" between 1999 and 2002 (Figure 4). The same coincidence was observed for the high level stabilization period after 2002, where weighted mean "available food" was stable at low levels. Thereby, the fraction of weighted mean "available cod" of total weighted mean "available food" was especially low, i.e., 2.2% in the third quarter of 2001.

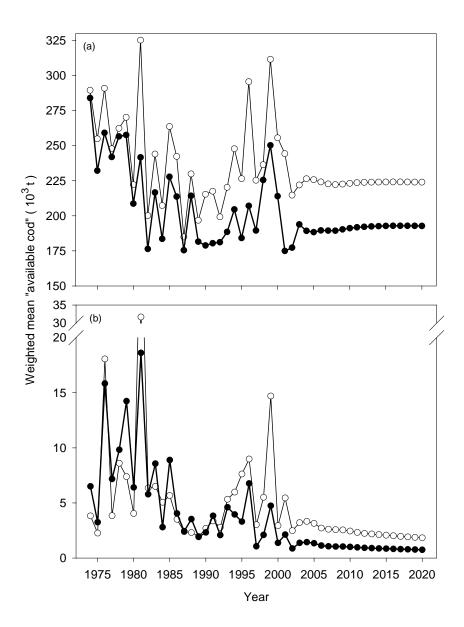


Figure 4: Weighted mean "available food" (a) and "available cod" (b) from 1974 to 2020 for all predators of the 2001 predator field which prey on cod (*Gadus morhua*). The weighted means originate from the predator specific mean "available food" ad "available cod" values that were calculated from the 47 simulations where the constant predator stocks of 2001 preyed on each of the different "available food" situations between 1974 to 2020. The proportional contribution of every 2001 predator stock and predator age group to the total predation mortality of cod age 0 calculated was chosen as the weighting factor. Note that there is a break in the y-axis of plot b) to display the trend more clear. \bigcirc : quarter 3. \bullet : quarter 4.

Historic cod and whiting recruitment variability (Analysis 3)

In the time period from 1965 to 2001 there were three sub-periods when in the 1st quarter relatively low cod age 1 recruit abundances coincided with relatively high abundances of larger grey gurnards (depicted as age ≥ 2 in Figure 5) and vice versa. The first period started after 1967 and ended in 1971, the next period occurred from 1976 to 1981 and the third and most pronounced period started in 1990 and is still ongoing.

The correspondence between whiting age 1 and larger grey gurnard anomalies resembled the pattern for cod and grey gurnard. Periods of decreasing grey gurnard abundance coincided with increasing numbers of whiting age 1 recruits, which then decreased once grey gurnard stock numbers sharply increased, e.g., in the early 1970s and 1980s. After the onset of the rapid increase of grey gurnard stock numbers in 1988 whiting recruitment at age 1 never came back to positive anomalies (Figure 5).

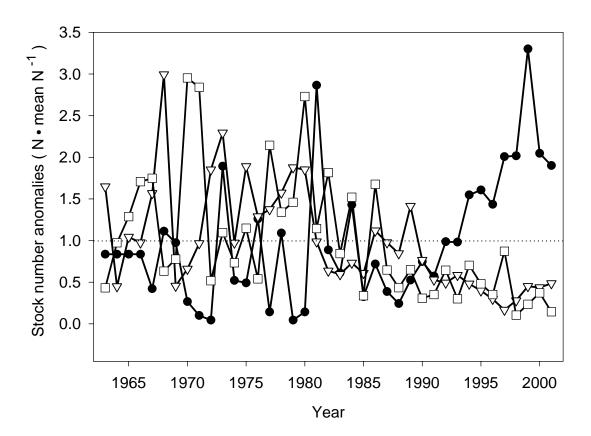


Figure 5: Stock number anomalies of grey gurnard (*Eutrigla gurnadus*, age ≥ 2 , •) and cod (*Gadus morhua*, age = 1, \square) and whiting (*Merlangius merlangus*, age = 1, ∇) in the first quarter of the years 1963 - 2001. Cod and whiting stock numbers originate from Multi Species Virtual Population Analysis (MSVPA) keyrun 2003 without grey gurnard as other predator. Grey gurnard stock numbers are the MSVPA 2002 input data.

The correlation analysis between the logarithmic cod age 1 quarter 1 recruit abundance and the logarithmic stock size of age 3 grey gurnard in the third quarter of the previous year revealed a significant negative correlation (1968–2001; Pearsons correlation coefficient r=-0.535, $p \le 0.001$, Figure 6). Including grey gurnards of age 2 lowered the significance to the 5% threshold (r=-0.336, p=0.052). When age 1 grey gurnards were included, the correlations lost their significance. Cod SSB and the abundance of age 3 grey gurnard in the first quarter was significantly negatively correlated (r=-0.553, $p \le 0.001$). The respective correlations

tion analysis between the logarithmic whiting age 1 quarter 1 recruit abundance and the logarithmic stock size of age 3 grey gurnard in the third quarter of the previous year revealed an even higher significantly negative correlation (r = -0.681, $p \le 0.0001$, Figure 6).

The negative correlation with the combination of age 2 and age 3 grey gurnards was still significant at $p \le 0.0001$ (r = -0.653). Whiting SSB and the abundance of age 3 grey gurnard in the first quarter was significantly negatively correlated (r = -0.504, p = 0.002).

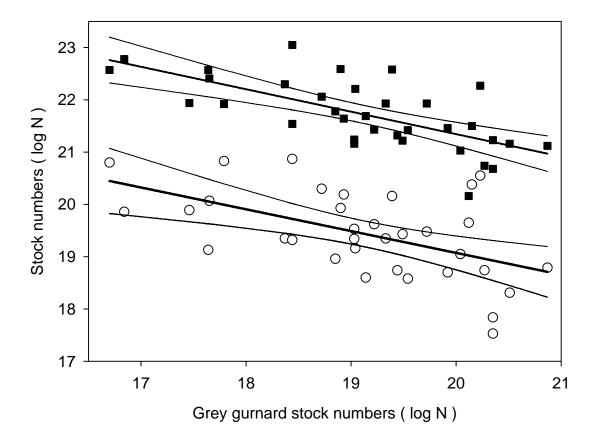


Figure 6: Stock numbers of cod (*Gadus morhua*) [log N] age = 1; O) and whiting (*Merlangius merlangus*) [log N] (age = 1; \blacksquare) in the first quarter of the years 1964 - 2001 as functions of grey gurnard (*Eutrigla gurnadus*) [log N] (age = 3) stock numbers in the third quarter of the previous year. Cod and whiting stock numbers originate from Multi Species Virtual Population Analysis (MSVPA) keyrun 2003 without grey gurnard as other predator. Grey gurnard stock numbers are the MSVPA 2002 input data. Lines depict linear regressions and corresponding 95% confidence intervals. Linear regression for whiting: r2adjusted = 0.447, p \le 0.0001. Regression for cod: r2adjusted = 0.264, p \le 0.001.

The GLMs fitting the 1st quarter cod age 1 stock numbers as a function of grey gurnard age 3 abundance anomalies in the previous third quarter, explained almost 30% of the total deviance. Thereby, it did not make a difference whether the cod age 1 stock numbers originate from the MSVPA 2003 keyrun without (model versions A) or with (versions B) grey gurnard included as "other predator" (Table 3, GLM No 1A, 1B), because grey gurnard prey almost exclusively on 0-group cod. In the GLMs without cod SSB as explaining variable, the negative effect of grey gurnard age 3 abundance anomalies in the previous third quarter was highly significant (Table 4).

When 1st quarter cod SSB in the previous year was taken as explaining variable instead of grey gurnard, the models explained 46% of 1st quarter cod age 1 recruitment (Table 3, GLM No. 2A, 2B). In the GLMs without grey gurnard anomalies as explaining variable, the positive effect of cod SSB was highly significant (Table 3). When both explaining variables were used together in a single model, grey gurnard always lost its significance (Table 4, GLM No. 3A, 3B,). The full models with both variables explained only 3% more than the pure cod SSB model (49.5% of the total deviance, Table 3, GLM No. 3A, 3B).

Table 3: Explained deviances of the cod (Gadus morhua) Generalised Linear Models (GLM).

GLM No.	1 A	1 B	2A	2B	3A	3B
Null deviance	24.148	24.048	24.148	24.048	24.148	24.048
(Deg. of freedom)	(37)	(37)	(37)	(37)	(37)	(37)
Residual deviance	16.979 (36)	16.886	12.921	12.883	12.187	12.140
(Deg. of freedom)		(36)	(36)	(36)	(35)	(35)
% Explained deviance	29.7	29.8	46.5	46.4	49.5	49.5

Table 4: Results from Type III ANOVA, testing the significance of the variables in the cod (*Gadus morhua*) Generalised Linear Models (GLM). 1) depicts the first variable in a model and 2) the second variable in a model. A: independent data sets. B: dependent data sets. Df: degrees of freedom. P(F): significance level. SSB: spawning stock biomass.

GLM No.	VARIABLE	DF	SLOPE	SUM OF SQUARES	F VALUE	P(F)
1 A	Grey gurnard	1	-0.437	7.168	15.199	0.0004
1 B	Grey gurnard	1	-0.437	7.162	15.269	0.0004
2 A	Cod SSB	1	0.994	11.227	31.278	< 0.0001
2 B	Cod SSB	1	0.991	11.165	31.200	< 0.0001
3 A	1) Cod SSB	1	0.807	4.792	13.763	< 0.0001
3 A	2) Grey gurnard	1	-0.174	0.734	2.108	0.1554
3 B	1) Cod SSB	1	0.803	4.746	13.682	< 0.0008
3 B	2) Grey gurnard	1	-0.175	0.743	2.141	0.1523

In case of North Sea whiting, grey gurnard age 3 abundance anomalies in the previous third quarter explained over 44% of the total variability in the 1st quarter whiting age 1 recruitment, taken from the MSVPA 2003 keyrun without grey gurnard (Table 5, GLM No 4A). A positive anomaly of age 3 grey gurnards in the third quarter of the previous year had a highly significant negative effect on 1st quarter age 1 whiting recruit numbers (Table 6, GLM No 4A). When whiting recruit numbers were taken from the MSVPA 2003 keyrun with grey gurnard included as "other predator", the explained deviance of the GLM was reduced to 34.1% (Table 5, GLM No 4B).

GLMs trying to explain 1^{st} quarter age 1 whiting recruitment as a sole function of whiting SSB resulted with explained deviances of 21% and 8.4% (Tab. 6, GLM No 5A, 5B). So, when the time series of whiting recruits originated from the independent data set derived from the MSVPA without grey gurnard included as predator, the explained model deviance by SSB was 2.5-fold higher, but still at a low level. Whiting SSB taken from the MSVPA with grey gurnard included did not have a significant effect on the explanation of whiting recruitment variability (p = 0.078, Table 6, GLM No 5B), because grey gurnard predation, (on whiting age 0 and 1) overruled the SSB effect.

When the two independent explaining variables were used together in a single model, only grey gurnard revealed a highly significant effect (Table 6, GLM No. 6A). In case of the independent whiting and grey gurnard data sets, the full model with both variables explained only 2.3% more than the pure grey gurnard model (46.4% of the total deviance, Table 6, GLM No.

6A). In the full model of the dependent data sets, the inclusion of whiting SSB did not increase the explained deviance of the model (Table 6, GLM No. 6B).

Table 5: Results of the whiting Generalised Linear Models (GLM).

GLM No.	4 A	4 B	5 A	5 B	6 A	6 B
Null deviance	15.506	11.452	15.506	11.452	15.506	11.452
(Deg. of freedom)	(37)	(37)	(37)	(37)	(37)	(37)
Residual deviance (Deg. of	8.662	7.545	12.254	10.494	8.311	7.545
freedom)	(36)	(36)	(36)	(36)	(35)	(35)
% Explained deviance	44.1	34.1	21.0	8.4	46.4	34.1

Table 6: Results from Type III Analysis of Variance (ANOVA), testing the significance of the variables in the whiting Generalised Linear Models (GLM). 1) assigns the first variable in a model and 2) depicts the second variable in a model. A: independent data sets. B: dependent data sets. Df: Degrees of freedom. P(F): significance level. SSB: spawning stock biomass.

GLM No.	VARIABLE	DF	SLOPE	SUM OF SQUARES	F VALUE	P(F)
4 A	Grey gurnard	1	-0.427	6.844	28.442	< 0.0001
4 B	Grey gurnard	1	-0323	3.907	18.642	0.0001
5 A	Whiting SSB	1	0.805	3.252	9.555	0.0038
5 B	Whiting SSB	1	0.444	0.958	3.288	0.0781
6 A	1) Whiting SSB	1	0.304	0.352	1.481	0.2317
6 A	2) Grey gurnard	1	-0.373	3.943	16.607	0.0003
6 B	1) Whiting SSB	1	0.019	0.001	0.006	0.9384
6 B	2) Grey gurnard	1	-0.320	2.950	13.687	0.0007

Sensitivity of the cod stock predictions to grey gurnard's relative stomach content of cod age 0 prey and grey gurnard abundance (Analysis 4)

The predictions with F_{pa} as future fishing mortality showed different cod stock developments depending on the relative fractions of 0-group cod in the stomach contents of grey gurnard age 2 and 3 and on different grey gurnard stock reductions (Figure 7). With the original input data for grey gurnard abundances and stomach contents, cod was predicted to almost die out in the future (SSB in the year $2100 = 8.3 \cdot 10^3$ t). Using a 30% reduced grey gurnard stock abundance, cod spawning stock biomass was predicted to stay on its current low level (SSB in the year $2100 = 27.7 \cdot 10^3$ t). So, according to the predictions only a reduction of more than 30% of the grey gurnard stock would result in a long term recovery of the cod spawning stock biomass, although very low future fishing mortalities (F_{pa}) were already assumed in the predictions. However, also with a reduction of 50%, the future cod spawning stock biomass was predicted to be lower than B_{lim} (SSB in the year $2100 = 43 \cdot 10^3$ t; with $B_{lim} = 59.5 \cdot 10^3$ t, ICES, 2003b (reduced by 15% to match the single species assessment stock definitions)). With grey gurnard excluded from the model cod SSB is predicted to reach $100 \cdot 10^3$ t in the year 2100.

Similar cod stock developments were also found at 30% and 50% reductions in the fractions of cod age 0 prey in grey gurnard stomach contents. The resulting SSBs in 2100 were only slightly lower compared to those that resulted from grey gurnard stock number reductions of the same magnitude. But when grey gurnard was kept in the model but the cod fraction in grey gurnard stomachs was set to zero, cod SSB was predicted to reach 175•10³ t in the year 2100, i.e., 82% higher compared to the total exclusion of grey gurnard from the model.

In the scenario with a combination of 50% grey gurnard abundance reduction and 50% stomach content reduction and in the scenarios where grey gurnard did not prey on cod at all, spawning stock biomass was able to pass B_{lim} (SSB 2100 = 72•10³ t, respectively SSB 2100 =

 $100 \cdot 10^3$ t). But only in the scenario where grey gurnard was kept as a predator but did not prey on cod, B_{pa} (127.5 · 10³ t; ICES, 2003b (reduced by 15%)) could be passed in the year 2013.

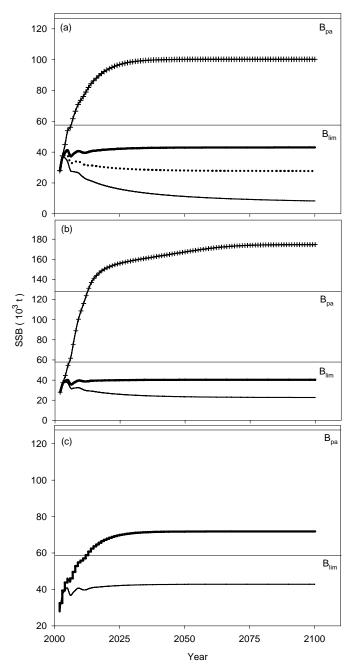


Figure 7: Predicted cod ($Gadus\ morhua$) spawning stock biomass development from 2002 until 2100. Cod precautionary (B_{pa}) and limit (B_{lim}) reference points are depicted as lines. (a) with different grey gurnard ($Eutrigla\ gurnadus$) stock number reductions; thin line: no reduction; dotted line: 30% reduction; thick line: 50% reduction; crossed line: grey gurnard excluded. (b) relative 0-group cod stomach content reductions; thin line: 30% reduction; thick line: 50% reduction; crossed line: 100% reduction. (c) combinations of (a) and (b); thin line: 30% reduction in grey gurnard stock numbers and 30% reduction in cod prey fractions in stomach content; thick line: 50% reduction in grey gurnard stock numbers and 50% reduction in cod prey fractions in stomach content.

Discussion

The design of the simulation

The task of Analyses 1 and 2 was to examine the Holling Type II functional response effect in the MSVPA model design. This could not be done by using real MSVPA model runs, because then changes in 0-group cod M2 caused by changes in predator abundance over time cannot be distinguished from the Holling Type II functional response effect. The isolated Holling Type II effect can only be assessed when the predator field is constant. The model results (prey abundances, total mortalities and suitabilities) were extracted and than used to externally calculate predation mortalities. This means that the M2 values did not originate from converged MSVPA model runs. Thus, the current approach can be seen as a simulation, analysing the Holling Type II effect in a multi species environment under boundary conditions that ensure the closest possible linkage to the North Sea MSVPA model. It can however be asked, how this exercise link to the real MSVPA model runs?

From the first analysis, the relation between 0-group cod M2 and cod abundance, the magnitude of the Holling Type II effect that occurred in the North Sea MSVPA could be deduced. If one would have taken any other predator field than that of 2001, the absolute M2 values would have been different, but the relative changes would have been exactly the same, because there is only a single relationship.

This also holds true for the second analyses, the relation between 0-group cod M2 and "available food". Here, changes in the predator field would as well result in absolute cod M2 changes, i.e., shifting the curve in Figure 2 in the direction of the y-axis. In addition the individual data points would be shifted in the x-axis direction, but still along the curve of a single relationship. This is because a relative change in the predator species composition leads to an equal change in the relative share that the predators partial M2s have on the total M2 of cod age 0, thus not changing the relationship displayed in Figure 2. The reason for this is that in the simulation the time series of "available food" is constant. So, for example when the sandeel stock in the North Sea collapses, which indeed may occur (ICES, 2005), and all other species in the ecosystem remain at their current levels, the 0-group cod M2 will increase, as the predators will increase the cod fraction in their diet composition when sandeel becomes less available. However, when the sandeel decline is compensated by an increase in herring biomass, the change in 0-group cod M2 will be less dramatic. The MSVPA model is able to mimic these ecosystem processes. The less the diet selection behaviour of the predators of North Sea cod is affected by changes in the potential prey field, the more realistic is the MSVPA model.

One could further ask, how the temporal variability in 0-group cod M2 (Analysis 2) would have changed with different reference predator fields? The temporal variability of 0-group cod M2 exerted by all predators which prey on 0-group cod, would still have been almost identical to the temporal variability of 0-group cod M2 exerted by grey gurnard. The reason for this is that the temporal development of "available food" for all predators which prey on 0-group cod, is almost identical to the development of the "available food" for grey gurnard. This in turn is caused by the fact that all predators which prey on 0-group cod, do indeed prey on almost the same prey types. That makes the temporal variability in 0-group cod M2 and of weighted mean "available food" rather insensitive to the choice of the reference predator field.

Uncertainties in the implementation of grey gurnard in 4M

The construction of the time series of grey gurnard stock numbers was based on the assumption of an availability of grey gurnards to the IBTS trawls which is comparable to those of the demersal gadoid group (Daan *et al.* 1990). An application of the average availability of the species cod, haddock (*Melanogrammus aeglefinus*), whiting and saithe (*Pollachius virens*) to

the English Groundfish Survey CPUES lead to an estimate of 204 000 t as average third quarter biomass of grey gurnard over the period 1977 to 1986. This figure was taken as the baseline for the construction of the input data time series. The method of deriving absolute biomasses from availability corrected survey indices (Sparholt 1990) is known to suffer from high inter-seasonal and inter-annual variability's in the calculated availabilities. However, as the species allocation of grey gurnard to demersal gadoids is reasonable and as both the survey time and the period of critical impact of grey gurnard on 0-group gadoids were the third quarter, the error shouldn't be too large. A size specific calculation of availabilities would for sure enhance the reliability of the biomass estimate. However, the current sensitivity analysis has shown that the trend in grey gurnard stock development is of greater importance than the absolute stock sizes, as even a 50% reduction in stock sizes did not enable cod to pass B_{lim} in the predictions. The trend has also been observed in the survey CPUES.

The second uncertainty in the implementation of grey gurnard in the MSVPA stems from the use of a single year of stomach content data set from the sampling year 1991. In 1991 the grey gurnard stock was at a rather low level, as was the cod stock. Since then the cod stock further decreased and the gurnard stock increased, which raises some doubts whether the spatial overlap between cod and grey gurnard would nowadays be still comparable to those found in 1991. In addition a single stomach data does not allow to assess whether grey gurnard displays prey switching, i.e., its predation on cod follows a functional response type III. If the latter would be true, the overall course of the cod stock predictions could be very different.

Why does cod go extinct in MSFOR predictions?

The current analysis revealed that the cod extinction in MSFOR predictions was not due to a model artefact: The functional response parameterisation of Holling Type II in the North Sea MSVPA was not responsible for the high 0-group cod predation mortalities at low stock numbers in the 1990s. In the multi species context, the increase in M2 for 0-group cod during the late 1990s (when cod stock numbers rapidly decreased) was rather dampened due to the parallel increase in total "available food". Instead the increasing grey gurnard biomass from the late 1980s onwards caused the increase in partial 0-group cod M2s, which is a volitional model behaviour as grey gurnard caused approx. 60% of the 0-group cod predation mortality. Grey gurnard did hardly influence the predation mortality of 1-group cod and older ages, as it preyed only to minor extend on 1-group cod in the first quarters.

The cause for cod going extinct in the predictions when grey gurnard is included in the model was the combination of low levels of total "available food" between 1999 and 2002 and increasing grey gurnard abundance. It could be shown in the simulations that the cod age 0 predation mortality inversely depended on the amount of total "available food" for all predators preying on cod. When looking at the stock developments of other major prey stocks in the North Sea, rather whiting, haddock and herring stocks and not cod itself caused this decline from 1999 to 2002.

Generally, in a multi species model such as 4M which is parameterised with a functional response type II, the rapid decline of a single stock which is small in relation to the total available prey biomass (as is the case for the North Sea cod stock), cannot lead to an over proportionally high increase in predation mortality of its recruits.

The effect of grey gurnard predation on historic cod and whiting recruitment

Both grey gurnard abundance and cod SSB significantly explained cod recruitment, when used separately. When both were applied in combination grey gurnard lost its significant impact. Cod SSB explained more variability in cod recruitment (approx. 45%) than grey gurnard stock numbers (approx. 30%). Grey gurnard abundances explained over 44% of the total vari-

ability in whiting recruitment, much more than whiting SSB was able to explain. When the two independent explaining variables were used together in a single model, both whiting SSB and grey gurnard stock numbers revealed highly significant effects. In case of the independent whiting and grey gurnard data sets, the full model with both variables explained only 2.3% more than the pure grey gurnard model (46.4%). The different explanatory power of grey gurnard for cod and whiting recruitment can have two reasons: 1) The impact of grey gurnard on cod recruitment was hidden because cod SSB and grey gurnard abundance showed a significant negative correlation. 2) Grey gurnard predation did impact differently on cod and whiting recruitment.

The first possibility cannot be assessed; however, whiting SSB was as well negatively correlated with grey gurnard abundance. Potential differences in the interaction processes can be deduced from the ecology of the species: in contrast to whiting, cod is a boreal species for which strong bottom-up effects of temperature (Planque *et al.* 2003) on and the planktonic environment (Beaugrand *et al.* 2003) recruitment are known. Hence, the historic increase in predation on 0-group cod by grey gurnard most likely supported the continuous decline in the North Sea cod stock due to fishing and environmental bottom-up effects. Whereas grey gurnard predation obviously was not a key factor for past cod recruitment, the current analysis demonstrated that this may have changed in recent years and especially that grey gurnard predation may play a key role for the future cod stock development.

A key to understand the differences between the interactions of grey gurnard and cod, and grey gurnard and whiting lies in the spatial distribution of the three species and lifestages: in the second and third quarters grey gurnards concentrated in frontal areas in the southern and eastern North Sea, as did small whiting, which in turn led to a significantly higher predator-prey overlap in high density areas of both, predator and prey (Floeter *et al.* 2004a). Small cod instead had a more shifted spatial distribution, offset from the high density frontal areas of grey gurnard. Hence, for cod the predator-prey overlap was lower and located in areas with lower grey gurnard biomass.

It is known from previous studies (e.g., Munk *et al.* 1995) that during their pelagic and settlement phase juvenile gadoids, especially cod and whiting, frequently occur in high numbers in frontal areas. From previous studies (Daan *et al.* 1990) and from own observations during LIFECO cruises in 2001 (Floeter, J., unpublished data) it is known that at least in the areas off Jutland grey gurnard undertake vertical migration during night time and feed heavily on pelagic 0-group gadoids. In another study, the spatial distribution of absolute consumption of grey gurnard was related to frontal areas in the second and third quarter 1991 (Floeter *et al.* 2004b). The average daily consumption of pooled fish prey (TL \leq 15 cm) was significantly higher in frontal areas, the average daily consumption of small whiting was also higher in frontal areas, but not statistically significant. This was not found for the consumption of cod.

Summarizing, this means that historic whiting recruitment was most likely more affected by top-down control due to grey gurnard predation than cod, because grey gurnard and whiting experienced a greater and more intense predator - prey overlap.

How does grey gurnard predation affect the future cod and whiting stock recovery potentials?

The sensitivity tests of the current analysis have shown that only in the prediction scenario with a combination of 50% grey gurnard abundance reduction and 50% stomach content reduction and in the scenario where grey gurnard was excluded, cod SSB was able to pass B_{lim} . In the scenario where grey gurnard was excluded, B_{pa} was almost reached. When grey gurnard was excluded from the model, both cod and whiting stocks increased in the predictions, but the cod stock increased approx. twice as much than does the whiting stock.

Instead, when grey gurnard was kept in the model but the cod fraction in grey gurnard stomachs was (unrealistically) set to zero, cod SSB was predicted to reach the highest value in all prediction scenarios (175 •10³ t in the year 2100). This cod SSB was 82% higher compared to that resulting from the total exclusion of grey gurnard from the model. This means that a key result of these multi species model predictions is, that this secondary species-interaction effect could potentially increase the cod recovery potential by over 80%. When grey gurnard is kept in model but its predation on cod is lowered, the predation by gurnard on whiting increases. As whiting is an important predator on cod age 0 and 1, this kind of implementation of grey gurnard in the model would even help cod to recover, instead of leading to its extinction. This second order effect has only clear effects in the magnitude of 80% reduction of cod fractions in grey gurnard stomachs. The reason for this threshold triggering this second order effect being so high, lies in a circular effect: high 0-group cod predation mortalities create high recruits in the hindcast model runs. This changes the cod stock-recruitment relationship in the model, which is used for the predictions, towards higher recruitment at low SSB. But in the predictions these high recruitment numbers do only have a small effect on the future development of the cod SSB, because almost all recruits are eaten by grey gurnard at age 0. This means in turn that the cod stock is in trouble regardless whether grey gurnard is taken into account or not.

In this context it further should be noted that the reason why only cod but not whiting went extinct in the MSFOR predictions is that whiting entered the predictions with a much higher SSB. This was only due to some relatively good year classes in 1997 - 1999, which in turn created high recruitment success in the predictions via the implemented stock-recruitment relationship. Once whiting SSB falls back to low levels it can be expected to go extinct in the MSFOR predictions as well, when grey gurnard is implemented as it was in the 2002 keyrun.

How to proceed with the implementation of grey gurnard in a North Sea multi species assessment model?

An important argument to exclude grey gurnard from the MSVPA was the phenomenon that grey gurnard predation created very high age 0 third quarter cod recruitment in the hindcasts which were not found in the third quarter IBTS. But obviously most of the predation occurs during the pelagic phase of the 0-group gadoids, which means that the dominant part of the decline in a cod year class takes place before the recruits are caught in the bottom trawl gear of the IBTS. This critical predation process may be just hidden from our eyes. We do not know very much about the absolute year-class strength before the age 1 recruits show up in the first quarter survey. From the third quarter surveys it cannot be deduced whether the North Sea MSVPA is able to capture the dynamics in the 0-group lifestages reliably.

The current analysis has demonstrated that a correct implementation of grey gurnard in the model is required to reliably assess the North Sea cod stock recovery potential.

To be able to define a correct implementation two key processes need to be understood: 1) Predator - prey overlap between cod, whiting and grey gurnard. 2) The nature of grey gurnard's functional response.

First, a spatio-temporal predator-prey overlap index would have to be explicitly coupled to the constant suitabilities, to take the obviously important spatio-temporal heterogeneity of the ecosystem at least partly into account. Second, a functional response parameterisation of Holling Type III (positive switching) would drastically reduce the predation mortality of prey stocks at low biomasses. This would most probably allow cod to recover in the model predictions. However, there currently is no biological evidence for a positive switching behaviour. Alternatively, the known increase in quarter 2 temperature since the early 1990s could have led to an increase in mean length at age of 0-group cod and whiting in the third quarter. This could have led to a reduced time span that 0-group gadoids dwelled in the narrow prey size

window of grey gurnard and hence led to reduced predation mortality. Then the positive effect of increased temperature would counter-balance the negative effect of increased grey gurnard abundance. In order to be able to answer these three key questions, a new full scale North Sea field program is needed.

In the meantime, the role of grey gurnard in North Sea multi species fisheries assessment should not be further neglected. Instead, alternative scenario predictions with reduced grey gurnard stock numbers and cod and whiting 0-group prey fractions in cod stomachs could help to define boundaries of likely cod and whiting stock projections.

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Annex 5: Are we able to model 0-group fish?

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Introduction

One main result of MSVPA calculations is that predation mortalities shows a large interannual variation especially for O-group fish (Magnusson 1995). In SSVPA this variability is ignored leading to differing recruitment estimates compared to the MSVPA approach. Since stock-recruitment relationships are a fundamental input for mid- to long term prediction scenarios (e.g., stock recovery plans) driving future stock developments, this translates directly into uncertainties in fish stock assessment. Also the calculation of reference points (B_{lim} , B_{pa}) for the precautionary approach to fisheries management is strongly dependent on the used stock-recruitment relationship (ICES, 1998).

Due to differences in recruitment estimates between SSVPA and MSVPA the question arises, which approach captures the interannual variability of historic recruitment better and should be used for fish stock assessment. MSVPA recruitment estimates of 0-group fish depend to a large extent on the stomach data set (stomach data 1981 or 1991) used to parameterize the diet selection model (Kempf 2003). This is against the assumption of constant suitabilities and reflects the uncertainties in 0-group recruitment estimates with MSVPA.

The second question which arises in this context is, whether we are able to model 0-group fish and their highly variable mortality rates at all. Or in other words, could the exclusion of 0-group fish and so a modelled recruitment at age 1 lead to more stable model results or would this exclusion lead to the loss of important information on interannual variations in recruitment success?

To answer these questions, recruitment estimates (age 0 and age 1 recruits) of different species from four different runs (Single Species, MSVPA Keyrun 2003, run 1981, run 1991) will be tested against an index derived from IBTS survey data. Ricker (1954) stock- recruitment relationships will be fitted for all hindcasts to calculate the explained variance between SSB and recruitment numbers at both defined recruitment dates (age 0 recruitment in the 3rd quarter of year t; age 1 recruitment in the 1st quarter of year t+1). For the three MSVPA runs correlation coefficients between age group 1 and age group 0 will be calculated to analyse the importance of the modelled 0-group fish predation mortalities for recruitment success. In prediction runs with different stomach data sets (stomach data 1981 or 1991) the importance of the not modelled variablity in suitability coefficients between 1981 and 1991 on future stock development will be analysed in addition. Finally the predictive power of multi species and single species approaches for recruitment estimates will be tested by making a time series split analysis.

Material and methods

VPA model runs carried out

Four VPA model runs were carried out with 4M (Vinther *et al.*, 2002). One model run was exactly the 2003 key run of the multi species study group (ICES, 2003). Two other MSVPA

runs differed in the choice of the stomach data set otherwise they were completely identical. One model run was parameterized with the 1981 stomach data only (run 81), for the other one only the 1991 stomach data (run 91) were used. All "other predators" (stock abundances are given as external input) were excluded from these runs since for most of these predator species (e.g., grey gurnard, raja radiata) only stomach data from 1991 are available. The inclusion of "Other predators" would make comparative analyses between run 81 and run 91 impossible. Finally, cod (gadus morhua), whiting (merlangius merlangus), haddock (melanogrammus aeglefinus), herring (clupea harengus), sprat (sprattus sprattus), Norway pout (trisopterus esmarckii), sandeel (ammodytes spec.) and saithe (pollachius virens) could be included in theses two runs. The fourth run was a single species run identical to the standard run used for evaluating differences between single species and multi species cod recovery scenarios at the 2003 study group meeting (ICES, 2003). To stabilize the results for the terminal years a multi species VPA tuning was carried out according to the method described in Vinther (2001) for each run.

Recruitment estimates vs. IBTS index

From the four hindcasts carried out, 0-group and 1-group stock numbers at the 3rd quarter or 1st quarter respectively were extracted for every hindcast year. From IBTS data the mean number of age 0 and age 1 fish caught per hour of every VPA species was calculated (see equation 1). IBTS data are only available for the 3rd quarter since 1991. This determined the starting year of the time series analysed. Year 2000 was chosen as terminal year for both recruitment dates.

1)
$$IBTS_{Index} = \frac{\sum_{x=1}^{n} number \ caught \ per \ hour \ of \ species_{i} \ in \ hol_{x}}{number \ of \ hols \ with \ species_{i} \ caught \ (n)}$$

For the recruitment estimates of the 4M hindcasts as well as for the IBTS index , anomalies in recruitment strength were calculated by subtracting the mean over the analysed time series. A Pearson correlation coefficient was calculated between anomalies in VPA recruitment estimates of every hindcast and the anomalies derived from the IBTS index.

Fitting of stock-recruitment curves

To test whether age 0 recruits show a stronger relationship with SSB in the different hindcasts than age 1 recruits, Ricker stock-recruitment curves were fitted for all VPA species at both recruitment ages with a non-linear regression using the Levenberg Marquardt algorithm in SPSS. Resulting R square values for the fitted stock-recruitment curves were compared for both recruitment dates in the four hindcasts. Higher R square values for age 0 recruitment would indicate, that the modelling of 0-group fish improve the precision of recruitment in mid- to long-term predictions, but do not allow any judgement on their correctness regarding its correspondence with reality.

In addition differences in the fitted stock recruitment curves between the four runs at both recruitment dates were analysed for species of interest.

Correlations between age 0 and age 1

To analyse the importance of modelled 0-group predation mortalities for recruitment success, a Pearson Correlation Coefficient was calculated for each of the three MSVPA runs between anomalies in age 0 recruitment and anomalies in age 1 recruitment. A strong correlation would mean, that in the model the recruitment success is already determined in the beginning of the 3rd quarter at age 0 and the modelling of 3rd and 4th quarter predation mortalities is not able to improve our understanding of processes driving interannual recruitment variability.

Differences in forecasted stock development between run 81 and run 91

To show the effect of the not modelled variability in suitability coefficients on stock development, mid-term prediction scenarios from 2002 to 2010 were carried out with MSFOR using mixed combinations of input data from run 81 and run 91 (stock recruitment relationship, future fishing mortalities) and future predation mortalities derived from the different suitability matrices calculated in theses hindcasts (Table 1).

Table 1: Combinations of input data from the respective MSVPA runs and future predation mortalities derived from different suitability matrices.

STOCK – RECRUITMENT RELATIONSHIP, INITIAL STOCK NUMBERS AND FUTURE FISHING MORTALITIES USED (RUN)	SUITABILITY MATRIX USED (RUN)	NEW RUN
1981	1981	run 81
1981	1991	run 8191
1991	1981	run 9181
1991	1991	run 91

So, for example, a stock-recruitment curve fitted with the results of the run 81 hindcast was combined with the 91 suitability matrix to conduct the predictions (run 8191). By mixing these input data derived from run 81 and 91, changes in the higher trophic levels of the food web between hindcast and prediction time period of the same magnitude as observed in the field between 1981 and 1991 were simulated.

For all scenarios the future recruitment estimates were calculated by using the already fitted Ricker stock-recruitment curves (Ricker 1954). The constant future fishing mortality matrix applied, constituted of mean values of fishing mortalities calculated between 1999 and 2001 in the respective hindcasts. SSB developments were plotted for all prediction scenarios and analysed in contrast. The uncertainties for multi species mid-term predictions, resulting from the use of different suitability matrices and so from the unaccounted variability in the higher trophic levels of the North Sea food web, were pointed out.

Time series split analysis

To demonstrate the performance of current Single and Multi species approaches in predicting future recruitment, the hindcast time series (1963–2001) in every of the four runs was cut off at year 1991. For the period between 1963 and 1991 Ricker stock-recruitment curves were fitted for each run and recruitment date separately. Also all other input parameters for MSFOR were adjusted to the shortened time series. E.g. the constant future fishing mortality matrix applied, constituted of mean values of fishing mortalities calculated between 1989 and 1991 in the respective hindcasts.

Mid-term prediction runs from 1992 to 2001 were carried out with MSFOR. Anomalies of predicted age 0 and age 1 recruits were calculated as described before and correlated to the IBTS index anomalies of age 0 and age 1 catches.

Results

VPA estimates vs. IBTS index

Correlations between anomalies in VPA recruitment and anomalies in the IBTS index were of a similar strength in all four runs with some exceptions especially for age 0 recruits (Table 2). The single species run had a higher Pearson correlation coefficient especially for herring and whiting than the MSVPA runs. Only run 91 herring age 0 stock estimates were able to reach a similar highly significant correlation with the IBTS index anomalies (run91= 0.731**; Single species= 0.861**). For haddock the correlation coefficient was high and significant in all four runs (> 0.7) while for cod, Norway pout, and sprat the correlation was only weak (< 0.4) and not significant.

Clearly higher correlation coefficients were calculated for age 1 recruits than for age 0 recruits in all runs (Table 3). In run 2003 and the single species run five of the six species tested had a significant positive correlation with the IBTS index anomalies for age 1 with correlation coefficients higher than 0.6. In run 81 and 91 four of six species had a significant positive correlation. Only cod showed a non significant correlation in all runs. The similarities between the runs were also higher than for age 0 recruitment estimates.

Table 2: Pearson correlation coefficients between VPA age 0 recruitment anomalies and IBTS index anomalies between 1991 and 2000.

	RUN 81	RUN 91	RUN 2003	SINGLE SPECIES
Cod	0.371	0.246	0.368	0.337
Whiting	-0.151	-0.118	-0.014	0.365
Haddock	0.709*	0.843**	0.925**	0.965**
Norway pout	0.117	0.225	0.208	0.163
Herring	0.546	0.731**	0.389	0.861**
Sprat	0.301	0.198	0.081	0.18

^{*} significant on the 0.05 level

Table 3: Pearson correlation coefficients between VPA age 1 recruitment anomalies and IBTS index anomalies between 1991 and 2000.

	RUN81	RUN91	RUN2003	SINGLE SPECIES
Cod	0.54	0.512	0.52	0.51
Whiting	0.91**	0.90**	0.914**	0.784**
Haddock	0.939**	0.963**	0.961**	0.968**
Norway pout	0.754*	0.771*	0.762*	0.825**
Herring	0.487	0.711*	0.724*	0.681*
Sprat	0.649*	0.574	0.635*	0.637*

^{*} significant on the 0.05 level

Differences in fitted Ricker stock-recruitment relationships between the four runs

The differences were exploratory analysed for cod, whiting and sandeel (Figure 1). Especially the stock-recruitment curves calculated out of run 91 age 0 recruitment estimates provided much higher recruitment numbers at a given SSB than the stock-recruitment relationships fitted in run 81, 2003 or the single species approach for these three species. The slope at the beginning of the stock-recruitment curves was different for the four hindcasts. Also the shape of the stock-recruitment curves varied between the model approaches. The carrying capacity for sandeel was reached at different SSB values. Run 2003 calculated still increasing recruitment numbers above a SSB of 1 million tonnes while run 91 was already on the right hand side of the Ricker stock-recruitment curve, for example.

For age 1 recruits the stock-recruitment curves of the four runs were more similar to each other than for age 0 recruits, especially for cod. The slope at the beginning as well as the shape of the curves showed a reduced variability between the four VPA approaches also for whiting and sandeel.

The already described differences in Ricker stock-recruitment curve parameters as well as the differences for other VPA species can be taken out of Table 4.

^{**}significant on the 0.01 level

^{**}significant on the 0.01 level

Table 4: Parameters of the fitted Ricker stock-recruitment curves for the different runs and species at age θ and age 1 recruitment:

SPECIES AGE		α				β			
SI ECIES AG	AGE	run 81	run 91	run 2003	ss	run 81	run 91	run 2003	SS
Cod	0	7.54	55.87	14.82	15.66	8.6E-10	9.9E-10	2.1E-09	3.28E-09
	1	2.89	2.85	3.66	4.16	9E-10	1.4E-09	1.8E-09	3.39E-09
Haddock	0	165.81	205.59	186.56	123.84	6.7E-10	1.3E-09	1.2E-09	2.05E-09
	1	36.86	11.08	26.8	40.49	8.2E-10	1.3E-09	1.2E-09	1.95E-09
Herring	0	63.79	45.35	61.54	110.47	3E-10	8.5E-10	7.1E-10	9.03E-10
	1	31.32	22.03	20.89	33.24	3.3E-10	7.6E-10	5.6E-10	7.77E-10
Norway pout	0	568.7	817.44	797.94	945.68	1.8E-09	4.3E-10	4.4E-10	2.3E-09
	1	315.38	215.71	234.9	414.63	2.3E-09	3.4E-10	3.1E-10	2.36E-09
Sandeel	0	1197.82	2624.2	1245.64	1052.95	9.7E-10	1.1E-09	6.3E-10	5.54E-10
	1	697.54	352.83	438.87	459.35	9.2E-10	7.1E-10	7E-10	5.54E-10
Sprat	0	180.48	384.57	410.1	260.12	1.6E-10	2.7E-10	3E-10	2.98E-10
	1	162.99	275.47	189.75	174.47	1.7E-10	2.9E-10	2.1E-10	3.08E-10
Whiting	0	56.98	125.86	72.57	78.49	2.4E-10	6.1E-10	7.1E-10	2.22E-09
	1	15.67	23.07	18.45	21.47	1.2E-09	8.4E-10	1.6E-09	2.33E-09

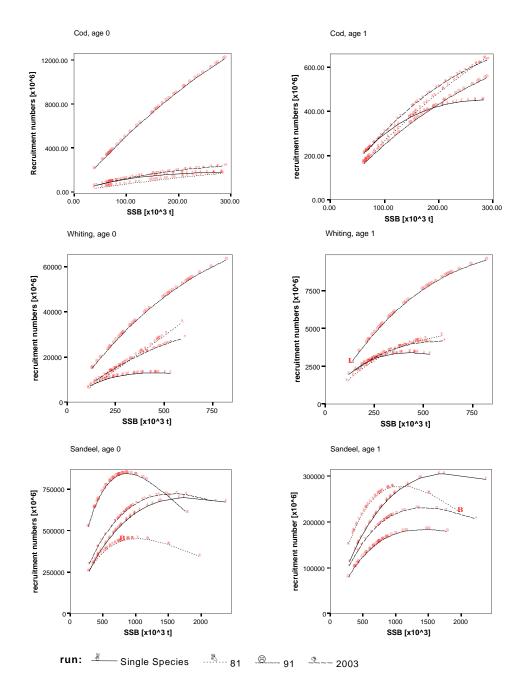


Figure 1: Fitted Ricker stock-recruitment curves for the different runs and two recruitment dates in the range of historic observed SSB values.

Differences in R²

The differences in r2 between Ricker stock recruitment curves fitted for age 0 and age 1 recruits were only small in all runs and for most species (Figure 2). Only for whiting and haddock a higher r2 for age 0 recruits could be reached at least for recruitment estimates of the MSVPA runs (e.g., run 2003: r2 for age 0 whiting= 0.3 but 0.09 for age 1 recruits). In general the relationship between SSB and recruits was slightly better in the MSVPA approaches than in the single species calculations. Especially the cases of haddock and whiting confirm this statement (e.g., r2 single species for age 0 whiting= 0.07; r2 run 81 for age 0 whiting= 0.51). The strongest stock-recruitment relationship was calculated for sprat in all four runs. The

weakest relationship was found for sandeel in the MSVPA runs and for haddock in the single species run. Most r2 values were under 0.4.

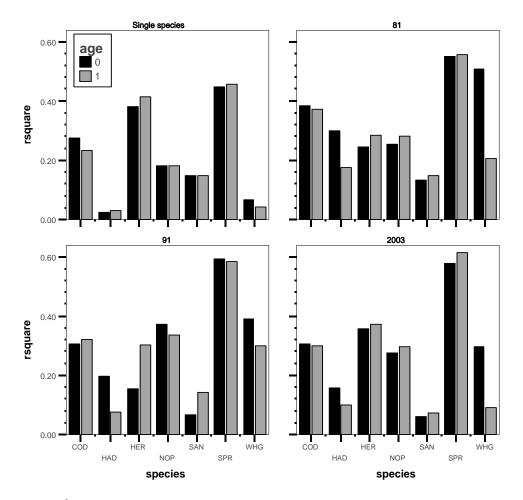


Figure 2: r² values of fitted Ricker stock-recruitment relationships for age 0 and age 1 recruits of different species in the four runs.

The importance of modelled interannual variations in 0-group predation mortalities for stock development

The correlation between age 0 and age 1 anomalies was of differing strength in the three MSVPA runs (Figure 3). While in run 2003 and run 81 age 1 anomalies were highly correlated with age 0 anomalies (Pearson correlation coefficient of 0.921** or 0.952** respectively) the correlation was much weaker in run 91 (0.511**). This means that only in run 91 the 0-group predation mortalities had the potential to alter the recruitment success of incoming year classes to some extent. Strong age 0 year classes could turn into weak recruitment years for age 1 after the 3rd and 4th quarter 0-group predation mortalities were effective and vice versa.

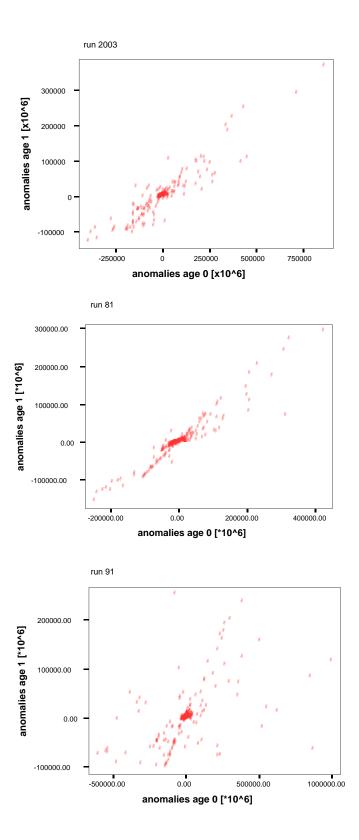


Figure 3: Anomalies in age 0 recruitment plotted against anomalies in age 1 recruitment for the different MSVPA runs and all VPA-species combined. Each single data point stands for anomalies calculated for a certain species in a certain MSVPA hindcast year.

Importance of not modelled interannual variations in predation mortalities for stock development

The observed distinctions in recruitment relationships and predation pressures between run 81 and 91 translated into different predicted SSB developments in mid term forecasts (Figure 4). The SSB of cod showed a slightly increasing trend in run 91 using the 91 suitability matrix and the corresponding stock-recruitment relationship $(59*10^3 \text{ t in } 2010)$ while in run 81 the trend was slightly negative $(27*10^3 \text{ t in } 2010)$. For whiting the differences were more pronounced. In run 81 the SSB was predicted to stay nearly on a stable level $(214*10^3 \text{ t in } 2010)$ while in run 91 whiting was driven to extinction until 2010. A similar picture can be drawn for Norway pout, which went extinct already in 2004 with the run 91 parameterization. For sandeel the sampled condition of the higher levels of the North Sea food web in 1981 using the 81 suitability matrix and the corresponding stock-recruitment relationship resulted in a strong decline until 2010 (SSB = $78*10^3$ tonnes), but the parameterization with the stomach data set of 1991 led to increasing stocks up to $1695*10^3$ tonnes until 2010.

When simulating changes between hindcast and prediction time period in the higher trophic North Sea food web of the same magnitude as sampled between 1981 and 1991, things changed again completely. The stock-recruitment relationship and fishing mortalities of run 91 together with the predation status sampled in 1981 led to a clear increasing trend of whiting SSB up to 441*10³ tonnes in 2009. As described before, without simulating a regime shift from the 1991 to the 1981 status of the higher trophic North Sea food web, the stock-recruitment relationship and fishing mortalities of run 91 led to the extinction of whiting until 2010 in contrast. When assuming a regime shift from 1981 to 1991, the situation for whiting worsened as compared to run 81. Comprising: changes in the condition of the higher trophic levels of the North Sea food web as sampled between 1981 and 1991 have the potential to reverse future SSB trends of whiting, mediated by the inserted stock-recruitment relationship and future fishing mortalities.

Also Norway pout showed the same pattern of stock developments. The predation mortalities calculated with the suitability matrix of run 81 together with the stock-recruitment relationship and future fishing mortalities of run 91 led to an explosive increase in Norway pout SSB (4335*10^3 t in 2010). The use of the 91 suitability matrix led to the extinction of Norway pout regardless from which hindcast the stock-recruitment relationship and fishing mortalities were used.

The same magnitude of differences between the prediction scenarios could be observed for sandeel. However, for this species the condition of the higher trophic North Sea food web in 1981 and not in 1991 resulted in a too high predation pressure leading to decreasing trends in calculated future sandeel SSB. For cod things were different: The choice of the stock-recruitment relationship had more influence on predicted stock developments than for the other species analysed. Using the stock-recruitment relationship of run 81 always led to decreasing trends in predicted SSB while the run 91 stock-recruitment relationship enhanced the recovery potential of cod regardless of the condition of the higher trophic levels of the North Sea food web. However, the level of predation pressure worsened or improved the recovery potential of the cod stock to a large extent.

So, for all species (with the exception of cod) the employed stomach data set and not the related stock-recruitment curve was the key force for the predicted stock development.

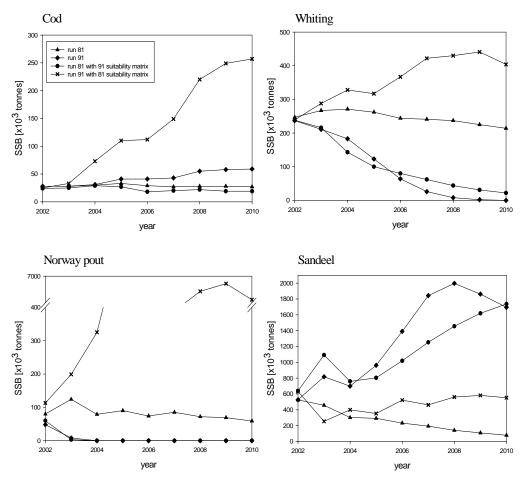


Figure 4: Predicted SSB development under the use of different combinations of input data from the respective MSVPA results and assumed future predation mortalities derived from different suitability matrices.

Predictability of recruitment anomalies

The predictability of recruitment anomalies between 1992 and 2001 turned out to be weak especially for age 0 recruits (Table 4). The anomalies between MSFOR age 0 recruitment predictions and the IBTS index anomalies were not significant correlated for all species in all runs except for whiting in run 2003. All other species had correlation coefficients under 0.4 or were even negatively correlated in 13 out of 24 cases. The correlation coefficients for age 1 recruits were in the same order of magnitude, however, negative correlations were only found for sprat and Norway pout in run 91 (Table 5).

Table 4: Pearson correlation coefficients between MSFOR age 0 recruitment anomalies and IBTS index anomalies between 1992 and 2001.

	RUN81	RUN91	RUN 2003	SINGLE SPECIES
Cod	0.352	0.383	0.146	0.098
Whiting	0.268	0.36	0.693*	0.283
Haddock	-0.068	-0.15	-0.081	-0.133
Norway pout	-0.041	-0.457	-0.479	-0.233
Herring	-0.137	-0.336	0.142	-0.126
Sprat	-0.32	0.341	-0.406	0.381

^{*} significant on the 0.05 level

Table 5: Pearson correlation coefficients between MSFOR age 1 recruitment anomalies and IBTS index anomalies between 1992 and 2000.

	RUN81	RUN91	RUN 2003	SINGLE SPECIES
Cod	0.065	0.053	0.068	0.067
Whiting	0.371	0.373	0.377	0.349
Haddock	0.139	0	0.174	-0.039
Norway pout	0.228	-0.006	0.244	0.344
Herring	0.357	0.28	0.347	0.385
Sprat	0.136	-0.567	0.143	0.137

^{*} significant on the 0.05 level

Conclusions

Performance of the different model approaches in hindcasting recruitment strength

For age 0 recruitment anomalies the single species approach showed a slightly better performance especially for herring than the MSVPA runs. For other species the correlation was low (e.g., for Norway pout, Cod) or high (for haddock) in all runs. So, a general conclusion which approach correlates better with the age 0 IBTS index anomalies could not be made. However, the modelling of 0-group predation mortalities in the multi species runs was not able to improve the correlations with the IBTS index.

For age 1 recruits also no strong differences between the single species and multi species approach could be found. But the correlation with the IBTS Index was better in all runs than for age 0 recruits. So either the ability to model age 1 recruits is higher than for 0-group recruits or the IBTS index for 0-group fish is worse due to problems with the bad catchability of 0-group fish, for example. The uncertainties for modelling age 1 recruits are smaller in any case.

^{**}significant on the 0.01 level

^{**}significant on the 0.01 level

Age 0 recruitment vs. age 1 recruitment

Since it turned out that the modelling of age 1 recruits is more certain the advantages and disadvantages of excluding the 0-group completely from the model must be discussed. The advantages are more stable model results and a better concordance with the IBTS index as independent validation tool. Two aspects would speak against the exclusion of 0-goup fish:

- A stronger stock-recruitment relationship for age 0 recruits than for age 1 recruits and so a better predictability of recruitment in the predictions
- 2) An important role of 0-group fish predation mortalities for recruitment success

The first point was analysed by fitting Ricker stock-recruitment curves to the different hind-cast results. Again the differences in parameters of the Ricker stock recruitment curves between the runs were smaller for age 1 recruits than for age 0 recruits leading apparently to more stable model results. When analysing the explained variance in the fitted stock-recruitment relationships by comparing r^2 values, the modelling of the 0-group brought mostly no advantages in terms of a stronger relationship with the SSB. The r^2 values for stock-recruitment curves of age 0 and age 1 recruits were similar despite for whiting and haddock in the MSVPA runs. For these species the r^2 values were higher for 0-group recruits than for age 1 recruits (e.g., run 2003 r^2 for whiting: age 0 = 0.3; age 1 = 0.09). This would indicate that the modelling of the 0-group improves the predictability of recruitment due to a better stock-recruitment relationship, however, only for these two species and only in the model world. The bad correlation of 0-group whiting estimates with the IBTS index challenges the use of this result.

In general, the multi species runs showed higher r² values than the single species run (e.g., r² single species for age 0 whiting= 0.07; r² run 81 for age 0 whiting= 0.51). But again, this finding rises the question whether the predictability of recruitment is really improved in MSVPA runs or if the stronger relationship is only an artefact of the model results and does not match reality since the single species approach shows the same performance in the correlation analysis with IBTS index anomalies.

So the final conclusions for this aspect are, that the MSVPA approach can slightly improve the relationship between SSB and recruitment at least in the model world. The currently applied modelling of the 0-group brings no advantages despite for whiting and haddock in the multi species runs.

The importance of the 0-group predation mortalities for recruitment variability were shown in two analyses. In the first analysis the importance was demonstrated by calculating correlation coefficients between age 0 and age 1 recruits. The high correlation coefficients in run 2003 and run 81 (0.92** or 0.95** respectively) mean that modelling the 0-group brings no advantages for explaining recruitment variability. In the hindcast the age 0 stock numbers are mostly only a direct function of the age 1 recruits in these two runs. So the modelled predation mortalities are not able to improve our understanding of processes driving recruitment success. The relative strength of an incoming year class is already determined at the beginning of the 3rd quarter and cannot be altered substantially by the 0-group predation mortalities. In predictions it makes therefore no difference whether age 1 or age 0 recruits are used as starting points for the modelled cohorts.

In run 91 a different picture is drawn. In this run the predation mortalities had the ability to alter the recruitment success. Strong positive anomalies for 0-group recruits could turn into weak age 1 year-class strength after the 0-group predation mortalities were effective and vice versa. According to run 91 the modelling of the 0-group would be an important part of every prediction scenario since the future stock development is mainly dependent on the survival rate of 0-group fish in MSFOR.

These results make clear that 0-group predation mortalities may have a strong effect on recruitment success, however, the differences between the runs are too strong to give a consistent picture. This raises the question what effect have the differences especially between run 81 and run 91 on recruitment success and how important is the not modelled variation in suitability coefficients for stock development.

This question was answered in a second analysis on the effect of using different stomach data in predictions. It could be demonstrated that top-down effects mediated by sampled changes in predator preferences and/or spatial predator-prey overlap as well as unaccounted changes inside "Other Food" can lead to substantial alterations in recruitment success. The number of 0-group survivors at different predation pressures (in turn caused by the use of different stomach data sets) determined the predicted stock development and the inserted stock-recruitment relationships calculated in run 81 or 91 hindcasts did not play a significant role (whiting, Norway pout and sandeel in Figure 5). The recovery potential of cod was also highly influenced by the top-down effects. Since the productivity coefficient α in the calculated stock-recruitment relationships varied to a large extent between both runs (e.g., reproductivity coefficient α for whiting in run 81 corresponds only to 39.75% of the α in run 91), this demonstrates the high potential of such changes in the food web as observed between 1981 and 1991. Unfortunately this variation in predation levels is not modelled what challenges the use of multi species recruitment estimates and predictions derived from the current model implementation.

So it turned out that modelling the 0-group is an important part of every mid- to long-term prediction scenario (e.g., recovery plans). However, a large part of the variability in 0-group survival rates is currently ignored by assuming constant suitabilities and so by ignoring sampled differences between the stomach data years 1981 and 1991 reflecting different ecosystem states. This makes MSVPA results uncertain and is a potential explanation why current multi species calculations are not able to improve the performance in modelling 0-group fish compared to the single species approach.

Performance of the different model approaches in forecasting recruitment strength

The predictability of recruitment turned out to be weak in all model approaches. The correlation between predicted recruitment anomalies and IBTS index anomalies between 1992 and 2001 were even negative correlated in 13 out of 24 cases for predictions with age 0 as recruitment date. The performance with age 1 as recruitment date was slightly better but also here all correlation coefficients were under 0.4 and not significant.

This bad performance is caused by a number of influences. First the fitted Ricker stock recruitment curves have low r² values for most species what mean that a lot of the variability in recruitment strength at a given SSB is smoothed out by using these curves in predictions. This challenges the use of stock-recruitment relationships with SSB as only explaining variable. The number of recruits entering the stock in the 3rd quarter at age 0 or in the 1st quarter one year later at age 1 is also determined by many other influences being effective especially during the first and second quarter of a year. These influences (e.g., climate forces, predation on fish larvae) are totally ignored in fish stock assessment in the North Sea so far. So any predictions made by using stock-recruitment curves are uncertain since recruitment numbers are an essential input parameter when predicting stock developments for more than two years in advance. The already discussed missing ability to model realistically the interannual variations in 0-group predation mortalities and so the survival rates of 0-group fish worsen the predictability of future stock development even more. Both described processes together with the unrealistic assumption of constant future fishing mortalities lead to wrong future SSB estimates what in turn lead to wrong recruitment numbers derived from the stock-recruitment curves. An ac-

cumulation of errors occur, making mid- to long-term predictions impossible with the current assessment tools.

So it becomes clear that we are not able to model the inter-annual variations in 0-group strength neither in the hindcast and more than ever in the forecast with the current MSVPA and SSVPA approach. However, it becomes also clear how important the modelling of 0-group fish is, since the whole future stock development is dependent on the recruitment numbers entering the stocks and on the survival rate of these recruits during the 0-group phase of their lives.

So it must be the aim to improve the ability to model the 0-group as most important live stage determining the future development of fish stocks. For this reason the MSVPA diet selection model must be improved by taking processes leading to the differences observed between 1981 and 1991 into account. Another big issue is the development of better stock-recruitment relationships which are able to reflect changes in stock reproductive potentials over time.

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